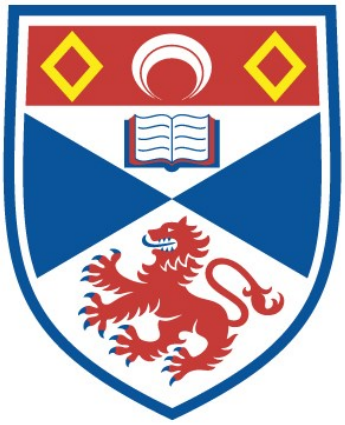
VISUAL AND BEHAVIOURAL INFLUENCES ON SONG TUTOR CHOICE IN ZEBRA FINCHES (TAENIOPYGIA GUTTATA)

Nigel Mann

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



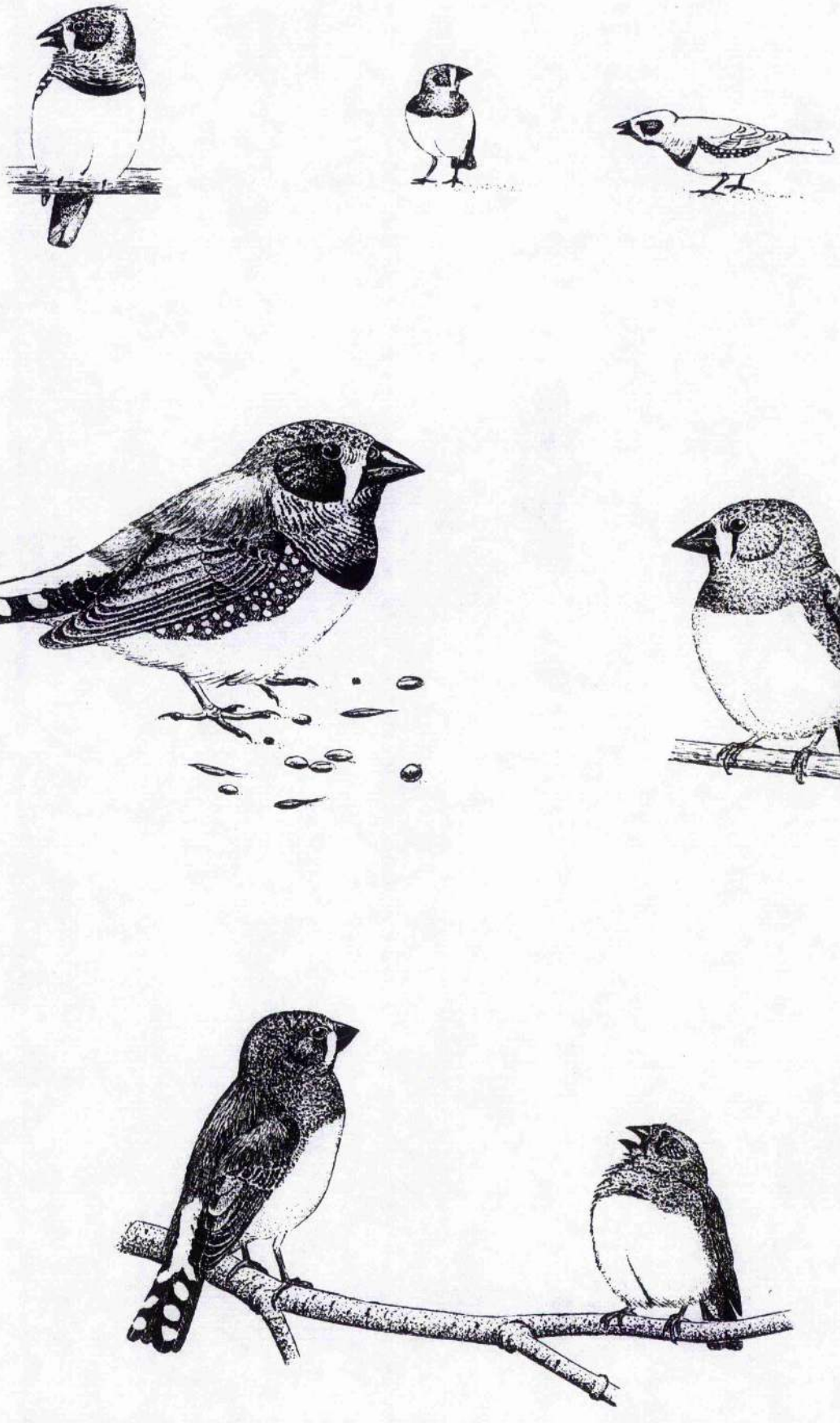
1992

VISUAL AND BEHAVIOURAL INFLUENCES ON SONG TUTOR CHOICE IN ZEBRA FINCHES (*Taeniopygia guttata*).

by Nigel Mann

Submitted in fulfilment of requirements for
the degree of Doctor of Philosophy.
University of St.Andrews, October 1991.

Th B137



CONTENTS

Acknowledgements

I received loads of help throughout the course of this thesis, much of it in the form of valuable encouragement at times when I needed motivating. There are therefore quite a number of people who I must thank.

First of all, I am very grateful to Peter Slater, who was always pleasant, always encouraging and who never seemed to lose confidence in me completing the thesis (though I must have caused some anxious moments as the submission deadline approached - sorry about that, Peter!).

I also received a great deal of help in terms of constructive comments from everyone else in the "behaviour discussion group", during the four-or-so years - particulary, Asep Adhikerana, Patrice Adret, Dick Byrne, Jeff Graves, Duncan Halley, Alex Jones, Frances Marsh, Jose Ortega, Fiona Povey, Kate Richards, Andy Whiten and James Williams.

Special thanks go to: James, for all the time he spent helping out with my computing problems, and particularly for writing a program used in chapter 6; Patrice, for working with me on the joint study, which formed chapter 6; Alex, Fiona and Frances, for helping a lot in the panicky time towards "the end", by typing for me and helping with figures e.t.c.; and Asep, for his computing help, and his "pep" talks.

The ethology group in Groningen also provided helpful advice during the enjoyable times that I spent with them.

I am grateful to everyone mentioned so far for the friendship they have shown me during my time in St.Andrews; getting through the PhD would have been very much harder without their support. This applies also to my good friends, Jim and Calla Cobb, and to others including Liz Slater and Ellen Graves.

I would also like to thank the department technicians, particularly Mary Tuchel and Sinclair Murray, for their willing and friendly assistance, Brian Jeffries for the cage building that he did for us, often at very short notice, and Dave Roach and Karen Johnstone from the photography unit for their advice and help.

Finally, to Sue (although I doubt she will read this), I would like to say thankyou for the immeasurable amount of help and support she has given over the years, without which I doubt that the thesis would ever have been completed. She willingly volunteered so many hours of her time to act as my unpaid research assistant. I wish her every happiness in the future.

ABSTRACT

Using a laboratory approach, this thesis further investigates patterns of song learning in the zebra finch (*Taeniopygia guttata*).

Chapter 1 provides a background to the form and function of song learning in a broad context, and introduces the zebra finch and the major role it has played in this field of research.

In Chapters 2 and 3, a strong influence of early visual imprinting on song tutor choice is demonstrated. Tutors of the same colour morph as the parents were much preferred. Song heard before or after the sensitive phase was often produced, if no tutor of the parental morph was present during this period. There was no clear evidence for one parent having a greater influence in this respect than the other. Differences were found between the morph preference for mates and song tutors, and possible reasons for these are discussed.

Chapter 4 revealed that the mother may influence tutor choice, probably by attentiveness to her by her offspring increasing their exposure to the song of an accompanying male. There was also a preference for a paired, rather than a single, male.

In Chapter 5, song tutor choice was studied in aviaries and related to behaviour occurring in this more naturalistic environment. A preference for learning the father's song was found; specific types of interaction did not link overall with song copying, but the amount of time that birds spent within close proximity did. General aspects of behaviour evident in the aviaries were are discussed.

The final chapter demonstrated that a short distance (38 cm) between tutor and tutee can be sufficient to inhibit song learning, probably because of the reduced scope for interaction.

I Nigel Ian Mann hereby certify that this thesis has been composed by myself, that it is a record of my own work, and that it has not been accepted in partial or complete fulfilment of any other degree of professional qualification.

Signed .. .. Date 23/10/91

I was admitted to the Faculty of Science of the University of St.Andrews under Ordinance General No 12 on OCT. 1987 and as a candidate for the degree of Ph.D. on NOV. 1988

Signed .. .. Date 23/10/91

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate to the Degree of Ph.D.

Signed .... Date 23/10/91

In submitting this thesis to the University of St.Andrews I understand that I am giving permission for it to be made available for use in accordance with the regulations of the University Library for the time being in force, subject to any copyright vested in the work not being affected thereby. I also understand that the title and abstract will be published, and that a copy of the work may be made and supplied to any bona fide library or research worker.

CHAPTER 1: GENERAL INTRODUCTION

This thesis is concerned with song learning in the zebra finch (*Taeniopygia guttata*), and in particular with some of the criteria which determine song tutor choice.

Before introducing the zebra finch, with the emphasis on its role in the study of song learning, I will review bird song learning in more general terms.

1.1 Bird song learning: patterns, causes and functions.

A wide variety of birds use "song" as part of their repertoire of communication methods, from the primitive divers (*Gaviidae*) to the more "advanced" passerines. It is the songs of the latter group (and especially of the oscine sub-order) that have received most attention by students of animal behaviour.

There are several reasons why oscine song (and, in particular, its ontogeny) has proved to be such a fruitful area of study for ethologists:

1) as an expression of animal behaviour, it is relatively easy to quantify and qualify. There is usually no problem in determining which of an oscine's vocalizations is its song, and the latter can be represented, and compared visually in the form of sonagrams (frequency versus time plots).

2) although there are obviously genetic factors intrinsic in it's development, oscine song is very much a learnt behaviour and thus is open to a wide variety of questions, such as "who do the birds learn from, and when do they learn?". It has been argued that the closely related sub-oscine group (*Tyranni*) do not need to learn their songs (Kroodsma 1984).

3) within the oscines, song performs a number of functions (the main ones being territorial defense and mate acquisition). Connected with this, there are several song learning strategies present; the latter may also relate, for example, to the ecology and the dispersal of the study species. All of this variety has added considerable interest to the study of bird song ontogeny.

4) song birds themselves are, amongst higher animals, particularly easy to study both in the field and laboratory conditions. They are of convenient size, are usually easy to keep and breed in captivity and they are diurnal and relatively overt in their behaviour.

That fully developed oscine song has to be learnt was established, in particular, by the work of Thorpe (1958), Marler (e.g. 1970) and Immelmann (e.g. 1969). They showed that song birds raised in acoustic isolation will produce an abnormal song (albeit, one that contains certain species-specific elements). This improvised song will be "structurally and communicatively deficient both as a territorial signal to other males and as a sexual signal to females" (Marler 1987).

Since the early work on bird song, a variety of further study techniques (as well as total auditory isolation) have been used extensively. These include isolating young birds, or exposing them to "song-tutors" or to tapes of song for specific periods, and deafening them at various stages of their song development.

There appear to be two main stages in the development of a bird's song: 1) memorization and 2) motor development. A young bird is believed by some to be born with a template (Marler 1970, 1976) which " can serve both as a kind of filter for focusing attention on sounds that match its crude specification, and as the vehicle for retaining information about the more detailed characteristics of sounds" (Marler and Mundinger 1971, from Bottjer and Arnold 1984). This template, still very much theoretical, will determine to some extent what can be learnt.

The "crude template" is responsible for the fact that, for example, tape recordings of both species played simultaneously to the young of the closely related and sympatric swamp and song sparrows (*Melospiza georgina* and *M. melodia*) will result in both species favouring their own songs (Marler and Peters 1977). In this case, male swamp sparrows base their choice on phonology, whereas song sparrows used phonological and syntactical (temporal organisation) cues.

During what is usually a fairly discrete period of time, learning (or memorization) occurs, in which the template is

"sharpened" by exposure to certain auditory stimulation from certain individuals, creating eventually a "fully formed template presumably [consisting of] some specific neural representation of the exact characteristics of the species-typical sounds heard during development" (Bottjer and Arnold 1984).

The motor development stage, which may or may not be widely separated in time from memorization, involves the transformation of the stored information into a well defined song by the matching of the bird's song output to the template. It begins with a period of "variable amorphous subsong" which may be important in learning how to use the vocal tract as an instrument for sound production (Marler 1987). There is then the "plastic song" phase when the motor rehearsal of songs occurs, followed by "song crystallization" - the development of a bird's completed vocal repertoire.

It has been found (in general) that deafening has very little effect on a bird's song after it has been crystallized, whereas deafening between memorization and motor development results in just basic amorphous song being produced. This indicates the importance of feedback in organising motor control. It is interesting that deafening in the canary (*Serinus canaria*) after song crystallization *does* have a dramatic effect (Nottebohm and Nottebohm 1978) but in this case the bird retains the song learning plasticity throughout its life.

In natural situations, a young bird is exposed to a plethora of noise, from which it must be able to pick out and learn the relevant sounds while ignoring the rest. The two questions that have most occupied ethologists are " when does the learning take place?" and "who does the young bird learn from?".

Taking the former question first, the term "critical period" was coined by workers such as Marler, Thorpe and Immelmann to describe the specific time (or times) in which memorization occurred. It became apparent that, for example, juvenile white-crowned sparrows required an exposure to adult males from 8-56 days if their songs were to be learnt (Marler 1970); chaffinches (*Fringilla coelebs*)were learning to some extent in their first few weeks, but also in their second spring, when they were starting to sing and to establish territories (Thorpe 1958, Slater 1983). Zebra finches also seemed to have a well defined early learning period (Immelmann 1969) while canaries had an age-independent "plasticity" and could learn new songs at any stage (Nottebohm and Nottebohm 1978).

It appeared at first as though only exposure to stimuli within the precisely defined "critical period" would result in a fully developed adult song. Marler 1970, for example, found that if he exposed previously isolated white-crowned sparrows to adult song at 100 days, they would still retain the song of total isolates and Immelmann (1969) similarly found zebra finches would not learn outside their "critical period". Terms such as "innate", "critical" and "absolute

irreversibility" were frequently used with respect to the timing of song acquisition very much in accordance with the ideas of Lorenz.

However, more recent work has refuted these claims that learning during these periods is irreversible once a stable preference is established (be it connected with song learning, or filial or sexual imprinting). Such preferences are to some extent plastic and can be altered, especially where the original stimulus was, in some way, poor (e.g. Bateson 1983, Eales 1985a,b). The stages of development in which a heightened response to stimuli occur are, nevertheless, genuine, but are now more reasonably termed "sensitive phases" (Immelmann and Suomi 1981, Bateson 1983). Lehrman (1970) is also very much against talk of innate-versus-learned aspects of behaviour, such as occurred in discussions of "critical periods" and song learning. He points out that it is meaningless to talk of some aspects of behaviour being either genetically determined, or alternatively, environmentally shaped, as "the ontogenetic development of species-specific behaviour often depends on environmental influence interacting with processes internal to an organism at all stages of development". It is this viewpoint that prevails today.

There have been a variety of situations in which song learning has been demonstrated to occur outside of a species' normal sensitive phase. For example, although marsh wrens and white-crowned sparrows (*Cistothorus palustris* and *Zonotrichia leucophrys*) will learn from tapes of their own

species they preferentially learn from a live tutor even if exposed to the latter after what would normally be the end of their sensitive phase (marsh wrens: Kroodsma and Pickert 1984; white-crowned sparrows: Baptista and Petrinovich 1986).

Some other factors that may affect whether the song of a bird encountered in the sensitive phase will be learnt, are as follows:

- the crude template filter more-or-less prevents the learning of a song of the wrong species (but see later with respect to sexual selection and repertoires). However, this can be overridden. For example, song sparrows can be "persuaded" to sing swamp sparrow elements by manipulating such elements into the song sparrow syntax (Marler and Peters 1977). In some species the template is not as discriminating as in others: for example, Thorpe (1958) noted that chaffinches can learn tree pipit (*Anthus trivialis*) song (both sound reasonably alike to the human ear).

- birds with a very low song output will probably not be used as tutors, although a bird can learn from a song that it has heard surprisingly few times (e.g. Petrinovich 1985, found that white-crowned sparrows can learn from just 120 songs).

- in the case of the marsh wren, day length has been shown to affect the sensitive phase, and thus whom the birds learn from (Kroodsma and Pickert 1980) and also the amount of song learnt in the first spring will depend on what had already been learnt in the previous year.

- in chaffinches and white-crowned sparrows late learning seems to be associated with the social stimulation provided by the singing territorial males (Slater and Ince 1982, Baptista and Petrinovich 1984). Social interactions, in fact, seem to play a big part in the song learning of many species, as we will see in zebra finches, and as also seems to be the case in indigo buntings, where young males copy from the male that they receive most supplanting attacks from (Payne 1981).

We now arrive at the question of which individual, or individuals, of its own species should a bird learn its song from?

In some cases song may indicate a measure of kinship. If birds learn from their own father then females could select males with songs of a certain level of similarity to their own fathers', in order to achieve an optimal inbreeding/outbreeding balance. Learning from the father has been reputed to happen in zebra finches (Immelmann 1969 etc.), as will pointed out later, bullfinches (Nicolai 1959) and Darwin's finches (Grant 1984, Millington and Price 1985). It is perhaps particularly important to achieve this inbreeding/outbreeding balance in such species as Darwin's finches, where the population has grown from a small number of founders in recent times.

Where song function is territorial it may be advantageous to delay song learning, at least in part, to the time when the young bird is itself setting up its territory (or shortly

after hatching if it will attempt to establish its territory close to the natal site). This is because it may well be important for a bird to learn from its neighbour, as is the case with indigo buntings (Payne 1981). This allows song sharing (and matching) to occur, resulting in increased breeding success (Payne 1981).

The situation with regard to whom birds learn from is quite complex. In some cases the father may not be chosen as a song tutor simply because the breeding system of the species in question is such that father-son contact is very brief, thus preventing such learning. This may be the case in various sparrows and the zebra finch.

In situations where song copying of neighbours is important, several strategies may be used as described by Slater (1989):

i) a bird may copy the whole repertoire of a neighbour's song so all songs are shared (white-crowned sparrows Baptista 1975, corn bunting *Emberiza calandra* McGregor 1980, village indigobirds *Vidua chalybeata* Payne 1985).

ii) birds may copy accurately songs chosen from a variety of individuals, so building up a unique repertoire (e.g. chaffinches, Slater et al 1980).

iii) birds may copy elements or syllables accurately but recombine them to make whole new sequences (e.g. winter wren *Troglodytes troglodytes* Kroodsma 1980).

iv) inaccurate copying at element or syllable level- this seems to occur in the zebra finch.

It is important to note that there is a difference between the songs learnt during the memorization phase, and the final song output. Individual birds may well have memorized far more songs than they will actually sing. Their final repertoire will be greatly affected by stimulation from females and other males (Marler 1987, Marler and Peters 1982): they might choose songs that match their rivals, or those preferred by females.

Brown-headed cowbirds (*Molothrus ater*) provide an example of the latter. West and King (1988) demonstrated that males selectively sing songs that solicit a "wing stroke" (precursor to copulation posture). Also they found that males' songs match those of the sub-species of the females with which they are housed, which suggests that they try many songs with the final selection depending on the female response.

Large song repertoires are also indicative of the rôle of female choice in male song learning. With great reed warblers *Acrocephalus arundinaceus*, females injected with oestradiol will respond only to long songs (Catchpole *et al* 1986).

In turn, preference for complex repertoires has resulted in an extended sensitive phase for song learning and has meant that the template in such birds is not the limiting factor

in what can be learnt. Instead there are motor limitations which could thus mean that large repertoires in birds like the great reed, marsh (*Acrocephalus palustris*) and sedge warblers (*A. schoenobaenus*) are a good indicator of male fitness.

Song learning studies in birds, apart from being of interest in their own right, have a more general importance that is worth pointing out. They provide an easily studied system that can link ethological study with the neural and physiological aspects of animal behaviour and much progress is being made in correlating the findings of these fields (see Bottjer and Arnold 1984, Nottebohm 1984, 1989, Clayton and Bischof 1989). Also, certain aspects, such as the contribution made towards the understanding of sensitive phases, have been shown to have relevance and application in the study of human behaviour (Bateson 1983).

1.2 Introduction to Zebra Finch Ecology.

Zebra finches belong to the family *Estrildidae* (which consists of the waxbills, munias, mannikins and allied species). There are about 125 species found in Africa, Southern Asia and Australia.

The zebra finch is sexually dimorphic in appearance, the male having orange cheek patches, white-spotted chestnut flanks, a broad black breast band and a red bill. The female has grey cheeks, no flank markings and an orange bill. There are 2 races of the species; the one inhabiting Australia

(*Taeniopygia guttata castanotis*) has fine black and white barring above the black breast band in the male, a feature that is absent from the "Timor zebra finch" (*T.guttata guttata*) occurring in the Lesser Sunda Islands. The "Timor" bird also uses different vocalizations.

The zebra finch is the most common and widely distributed of the grass finches in Australia, inhabiting the entire dry interior, while being absent from some wet coastal forests. The species can survive a wide range of temperatures from very hot down to about 6C. They are adapted especially to dry habitats, where rainfall is unpredictable. The latter has led to a breeding strategy whereby the birds are ready to mate and produce young immediately after rain showers.

Their habitat consists of areas of open steppe with scattered clumps of bushes and trees, often near watering places.

Zebra finches are colonial, gregarious and nomadic. The latter is thought to be the reason for the lack of geographical variation in the appearance of the Australian sub-species (Keast 1958); this reason has also been applied to the lack of dialects (Immelmann 1969).

Zebra finches feed primarily on grass seeds, but will also consume charcoal and small insects as well as foxtail millet and other vegetation.

The need to be able to breed at any time of the year has led to several adaptations. They apparently form lifelong pair bonds and have constant gonad activity. The breeding cycle is reasonably rapid; many broods can be raised in quick succession (Farner and Serventy 1960), while conditions are favourable. The young are independent by 35 days and in the case of males, have completed testis growth by 70 days. The female's ovaries are fully developed by six months, but they can breed earlier than this (Sossinka 1980). "Juveniles" may even attempt to breed in the same vegetative period in which they were hatched.

Another adaptation to the birds' arid, unpredictable environment is the slow continuous wing moult, very unusual in passerines (Zann 1985). The presence of this feature in the seasonal climate of Victoria is considered to be non-adaptive, indicating that zebra finches evolved elsewhere.

Zebra finches nest in breeding colonies of 5-25 pairs, with usually one pair occupying an individual bush. The breeding birds still feed, drink and bath together. The nest is built of rough grass and is lined with softer vegetation as well as feathers, rabbit fur, wool etc. There is usually a bottle-neck entrance tunnel. The male does most of the collecting for the nest, while both sexes help to build it. Outside the breeding season zebra finches also build "sleeping nests" that generally lack the entrance tunnel.

A good clutch generally consists of 3-8 eggs, light blue to white in colour. Brooding begins after the 4th or 5th egg is

laid and is done by both sexes. They hatch after 12-16 days, and all chicks emerge within 36 hours. They begin to fledge at 22 days, when parents and young learn to recognise each other by voice. The juveniles soon start moving around the colony, meeting up with other broods.

Zebra finch vocalizations include a variety of calls, used in circumstances such as flight and aggression, to maintain contact with a partner in a flock and during mating. There is also a "distance call", often associated with periods of activity such as taking off. It is most common in large groups, and has a high reply rate. The call is sexually dimorphic, the male's having a tonal and noise element, while the female's lacks the latter (Zann 1984). Unusual amongst bird calls, the males' distance call must be learnt by young birds; they need to be exposed to a conspecific male in the first 40 days if the call is to develop later (Zann 1984 and 1985). Brindley (1988) has shown also that individuals can recognise each other by their distance calls. Distance calls are often incorporated into the song of the male.

(Most of the information above was obtained from Martin 1985 and Immelmann 1965, 1969, 1972a,b).

1.3 Song Learning in Zebra Finches

Vocal learning starts very early with subsong usually beginning between 30 and 40 days (or even as early as 24, Immelmann 1969). The subsong consists of quiet bursts of

sound at irregular intervals. At first there is little sign of adult phrasing, and elements are included that are absent from the adult repertoire. At 40 days some elements are present which bear some similarity to each other, and that will be used in the crystallized song. At 60 days the final elements are recognisable and the sequence is repetitive. From then song length and tempo may increase and song phrases may be linked together into longer sequences.

This rapid song crystallization is one of the advantages of studying song learning in the zebra finch. Equally important factors are:

1) It is a widely kept cage bird.

2) It breeds readily in small cages throughout the year and is relatively easy to look after.

3) It has a very short generation time.

4) It has a brief repetitive song allowing for ease of analysis.

Zebra finches have two forms of song, directed and undirected. The former is used in courtship being "directed" at the female, and is sung at a higher tempo than the latter. It is associated with a courtship display in which the crown feathers are raised, the belly feathers are spread and the head is turned from side to side.

Undirected song is heard less often during pair formation, but this is not due to a time constraint (Caryl 1981), which implies that it is being inhibited. Instead it is used when a bird is not being influenced by any major motivational

state, suggesting that it is a low priority activity that fills spare time (Immelmann 1969, Caryl 1981). It may serve some function in individual recognition (Miller 1979a,b) and pair cohesion. Zebra finch song does not seem to serve any territorial function.

Zebra finch song learning was first studied in detail by Klaus Immelmann from 1969. In this paper Immelmann described the early start and end of the sensitive period for the acquisition of song elements. He asserted that the song learning closes during juvenile subsong, and that an "innate preference" for the song of the father, and for the right tonal quality was shown. Hence Immelmann concluded that zebra finches are birds that require close personal interaction with their tutor for learning to occur.

This was further demonstrated where zebra finches raised by Bengalese finches *Lonchura striata* (the domesticated form of a closely related species), were found to sing Bengalese not zebra finch song, even when they could see and interact with zebra finches. Only when a zebra finch male actually fed the young birds was a zebra finch song learnt.

Immelmann (1969) carried out experiments in which zebra finches were isolated during stages of their development, by rearing them by hand, or by females only. In such circumstances, when the isolation occurred in the first few weeks of life, the song of the male was found to consist of a small number of varied syllable types, and was longer in duration. The complex elements, increasing or decreasing in

frequency, were absent; also, female call notes were included when the birds were female-raised and the song tempo was slower than normal. This is equivalent to the pattern of the isolate songs of the chaffinch (Thorpe 1958) and blackbirds *Turdus merula* (Thielcke and Thieckle 1960). Immelmann commented that "the basic outline of song in Estrildids seems to be independent of experience".

Since this initial study by Immelmann, many others have involved further isolation experiments, more manipulations involving Bengalese finch foster parents and various detailed behavioural studies. Some of Immelmann's early assertions have not stood up in the light of this more recent work. He believed that the sensitive phase for song learning was a very rigid phenomenon occurring in the first few weeks of life, from 25 to 60-80 days, and out of this period nothing else could be learnt. He also maintained that, because songs were not likely to be learnt after independence, the father would normally be the song tutor.

It is now clear that imprinting of any sort during a period of heightened sensitivity is not irreversible (e.g.Bateson 1979 and 1983), particularly in circumstances where the sensitive phase stimulus is weak.

Eales (1985b) found that song is usually learnt between 35-65 days but that experience does matter. Zebra finch males will learn song beyond the 65 day limit if no suitable tutor has been presented. Furthermore, Clayton (1987a) showed that earlier song may also be recalled, if the zebra finches are

not provided with a suitable tutor in the sensitive period. This in itself shows that learning does occur before 35 days, but the elements learnt at this stage are not normally present in the final song.

The likelihood of the father being used as the tutor is also open to doubt, but the situation here is more complex. If the sensitive period is from 35-65 days, as seems to be the case, and if young birds become independent at about 35 days (Immelmann 1969) then it seems likely that the father's song will not be the one learnt. Indeed in experiments in which the young birds are exposed to an unknown "tutor" at 35 days, after being kept with their parents prior to this day, the tutor is almost always the bird chosen for song learning purposes (Eales 1985b).

Immelmann may have kept his young birds with their parents for too long. However, it is at the period of around 35 days that parents start attempting to chase off young birds from the nest area, sometimes very aggressively. As Clayton (1987b) showed, adult male aggression has a possible link to song tutor choice, and thus this brief period could have some significance in the ultimate song of the young finch. Furthermore, Böhner (1986), when he removed zebra finches from their parents at 35 days and isolated them, found that they would produce songs as similar to their father as if they had been removed at 100 days. Eales (1987b), also obtained similar results to these despite anticipating the development of little more than an "isolate" song, taking into account earlier results (Eales 1985b). The difference

probably relates to the fact that Böhner (1983) and Eales (1987b) kept their birds in visual (not acoustic) isolation at independence, whereas Eales' birds in 1985 were acoustically isolated, were therefore subjected to a lack of social stimulation and thus practice may have been inhibited or reduced.

Böhner (1983) kept young birds with their parents until 40 days and then gave them a choice of song tutor between their father and a strange male. In all but one case the father's song was learnt. Böhner postulated that the feeding of the young bird by its parents could be the cue for determining tutor choice. The exception to the pattern occurred where one of the neighbours sang 10 times more frequently than the father. Although this points to an important role of song output in song tutor choice, Clayton (1987b) found that the amount of singing, above a certain minimal threshold, had no effect on which tutor's song was selected.

Clayton (1987b) showed that birds separated from their parents at 35 days would always choose to copy the song of a bird sounding most similar to their father, and would tend, in particular, to copy elements that were shared with the father. This copying may in itself help contribute to an optimal inbreeding/outbreeding situation. For example, female zebra finches have been shown to be able to discriminate between their father and another male even if separated from the former at 25 days (Miller 1979a), and could thus presumably select as a mate a partner with a song differing by a certain amount from the fathers'. This song

discrimination might also be facilitated by the fact that males often have distance calls in their songs, and females have been shown to be able to recognise a certain individual's calls (Brindley 1988).

A further benefit of males either learning from their father, or from a male with a similar song to their fathers, would be that kin recognition would become easier. Although it has not yet been observed in the species, co-operation between kin is a possibility in colonial birds such as the zebra finch.

As mentioned earlier, Bengalese finches have often been used in studies on zebra finch song learning. In particular, people have been looking for the factors that ensure that a young bird copies its song from its own species rather than another, making use of the fact that Bengalese finches will readily foster a zebra finch brood. The zebra finches will invariably learn from their Bengalese foster parents if kept in the same cage with them, even if they can see and hear zebra finch adults (Immelmann 1969). However, if they are allowed to be in physical contact with a male zebra finch, they will often learn from him, even if they can still hear their Bengalese foster parent. The inverse is not true - if young zebra finches are raised by their own species, and are then put in a cage with a male Bengalese Finch, they will not learn the latter's song (Eales 1987a). This "own species bias" is a widespread phenomenon in studies of mate choice (e.g. Ten Cate 1982, Ten Cate and Mug 1984, Clayton 1987c) and song learning.

The bias could be due to a difference between the species at a genetic level- perhaps the crude template of the zebra finch especially facilitates the learning of its own species song. Slater, Eales and Clayton (1988) point out that Bengalese finches have song phrases that are generally longer in duration and number of elements than in zebra finch songs, and they often repeat elements within a phrase (zebra finches tend not to). Element structure is also different (zebra finches have up to 8 stressed harmonics whereas Bengalese usually have less than 4). In addition, zebra finches include species specific calls in their songs, which may act as labels. All of these characteristics may make Bengalese songs more difficult to learn, and this seems to be indicated by ten Cate's observations of listening behaviour (1986a), seen most often when young zebra finches are being tutored by Bengalese finches rather by than conspecifics.

However, experiments by Clayton (1988, 1989) seem to indicate that Bengalese finch song elements themselves are no more difficult to learn (although this would not discount the importance of phrase length, lack of repetition and the presence or absence of zebra finch calls). In the first of these studies (Clayton 1988) she provided young zebra finches (female-raised) with a choice of two tutors, one of which sang Bengalese elements, whilst the other sang typical zebra finch song. There turned out to be no preference for the latter.

Probably more significant than song type in this "own species bias" are the behavioural differences apparent between zebra finch and Bengalese "tutors". The possible relevance of aggression in song learning (Clayton 1987b) has already been pointed out, and certainly zebra finches show more aggressive behaviour (and also more parental behaviour such as brooding and feeding) than do Bengalese parents (ten Cate 1982 and 1984).

The importance of extensive social stimulation and interaction in zebra finch song learning is further emphasised by the failure until recently to teach young birds from song recordings. They even failed to learn from males heard "live" over an audio link, and will only "pick up" a few elements from a bird which they cannot see despite being able to interact vocally (Eales 1989). However, they have now been shown to be capable of learning from tapes, but only if they can manipulate their exposure to the stimulus by key pressing in order to hear the song (Adret, in prep.).

Before outlining the aspects of zebra finch song learning that I am personally involved in studying, I will firstly consider some of the interpretive problems that I may be faced with.

When studying captive animals there is always the problem of low external validity (e.g. see Altmann 1975). In other words it may be possible to determine a number of variables that may alter an animal's behaviour in the laboratory, by

means of experimental manipulation and control, but there are bound to be difficulties when trying to relate such "internal validity" to the situation in the animal's natural environment. Petrinovich and Baptista (1987) comment that "no laboratory situation can simulate the experience of young birds in nature to the extent that we can infer, relative to the timing of dispersal, when exactly this learning occurs".

Lorenz (in Bateson 1983) goes further by stating that as animals are not adapted to deal with such abnormalities, studies in captive conditions can only throw up "meaningless results". This point of view, however is very narrow and, in the case of song learning, it would have been impossible to have achieved anything like a comparable amount of knowledge of its timing and development without laboratory studies. There has to be a combination of field and laboratory study if a behaviour is to be fully understood.

Lehrman holds a contrasting viewpoint from that of Lorenz (also in Bateson 1983); he regards abnormal and normal as simply two ways of treating a developing organism and comments that "it is precisely by consulting changes resulting from environmental variation that you can arrive at understanding mechanisms of development".

Considering zebra finches in particular, there are several consequences of long-term domestication that may be relevant to the interpretation of laboratory results. With regard to behaviour, captive zebra finches show higher levels of

sexual behaviour but less extended courtship than do their wild counterparts, they have a shorter time for nest building and incubation, they show accelerated development of the young, they have a shorter generation time, they brood and feed their offspring irregularly and they show an increased level of contact between individuals (particularly parents and offspring) resulting in more aggression. White zebra finches are considered to exhibit especially "serious disturbances" in their behaviour and this, in turn, affects behaviour of other zebra finches toward them (Martin 1985).

In relation to song formation, Slater and Clayton (1990) have shown that St. Andrews zebra finches use fewer call notes in their songs than do those in the wild and in the captive population at Bielefield in West Germany.

1.4 Introduction to my research

The aim of this thesis was principally to investigate further the criteria on which song tutor choice is based in the zebra finch, by carrying out a series of laboratory-based experiments.

The first study (Chapter 2) considered the effect of visual imprinting on tutor selection, by using different colour morphs of zebra finch. Would zebra finches always choose a tutor of their parents' colour, if such a bird is present during the sensitive phase? Will they learn from an individual of the non-parental morph, if no other males can be seen in this period? Mate preference was also determined,

and the results for this and song tutor preference were compared.

In Chapter 2 both parents of each brood shared the same morph. In contrast, in Chapter 3 the mother and father were always of different colours, but otherwise similar questions were asked. In particular, an attempt was made to determine whether one of the parental sexes has a greater influence on the song tutor or mate choice of males, or on just the mate preference of females.

Previous work had revealed a strong preference for the father as song tutor, if he is present during the sensitive phase. In Chapter 4, experiments are described that further examine this preference. The possible influences of the mother and of paired tutors (unrelated to the tutees) are also considered.

In Chapter 5, a more natural set-up was used, by housing zebra finches in aviaries instead of small cages. The behaviour of the finches was monitored, mainly through the period 35-65 days, and related in the analysis to song tutor preferences. Emphasis was placed again on whether it is usually the father that is preferred as the song model.

It is becoming increasingly apparent that interacting and closely associating with a song tutor have an important rôle in the song learning process. If so, learning from a particular tutor is likely to be less complete when the tutor and tutee are kept some distance apart - results from

Adret (in prep.) have indicated that this is indeed the case. In Chapter 6, pairs of tutees were exposed to a tutor, with one separated from the adult by only a mesh partition, while the other was further separated by a gap of 38cm. The effect of this difference in proximity was related to the quantity and quality of song copied from the tutor. This experiment was carried out in collaboration with Patrice Adret.

Chapter 7 summarises the principal findings and conclusions of the thesis.

CHAPTER 2: THE INFLUENCE OF VISUAL STIMULI ON SONG TUTOR CHOICE IN THE ZEBRA FINCH

2.1 Introduction

Male zebra finches usually learn the song of an adult to which they are exposed in a short period early in life. This sensitive phase extends from about 35 to 65 days in our laboratory conditions (see review by Slater et al. 1988). Within this time period birds are most likely to learn, but they are also highly selective in their choice of tutor. Given a choice between their father (or foster-father) and a strange male, they prefer the former (Böhner 1983). They also prefer a bird sounding like the father to one with a dissimilar song (Clayton 1987b). They have been found to learn from the more aggressive of two tutors (Clayton 1987b), though this may simply represent a preference for the bird with which they interact most. Finally, they will prefer a Bengalese finch male tutor, instead of a zebra finch, if they have been reared by a pair of the former species (Immelmann 1969, Eales 1987a, Clayton 1988).

It is apparent that a variety of cues are likely to be involved in tutor choice. The findings given above suggest the importance of auditory information and of tutor behaviour. There has been no conclusive demonstration that visual cues alone, based on the morphology of potential tutors, can direct

choice. Such cues may be important where birds reared by Bengalese finches choose to copy from this species, but it could also be that the young zebra finches developed a preference for birds sharing certain behavioural characteristics with the birds that reared them.

Testing the possibility that visual cues as such are important requires that young birds are presented with a choice between individuals that differ only in this respect. We have done this in the experiments to be described here by using different zebra finch colour morphs as tutors. There are no obvious behavioural differences between these morphs, and the design can be balanced to allow for any slight differences that may exist.

Strong visual imprinting on the parental colour morph before 35 days has been shown by Immelmann et al (1978), using white and grey birds. The young birds subsequently showed positive assortative mating. Clayton (1987b) found no preference between grey and fawn birds as song tutors, but these morphs are relatively alike in appearance. Her study also involved varying many other possible tutor selection cues, so that any underlying effect could have been obscured. We chose to follow Immelmann and use birds of rather more dissimilar appearance. The study was concerned with the following questions:

a) does visual imprinting on the parent or foster parent prior to independence lead to a preference for that morph in song tutor choice?

b) does exposure only to a male of the unfamiliar morph during the sensitive phase affect song learning?

c) does early experience of a particular morph affect song learning and mate choice in equivalent ways?

2.2 Methods

STUDY ANIMALS

The birds used were of two morphs, grey (or wild-type) and chestnut-flanked white (see Figures 2.1 and 2.2). The latter was used rather than the pure white morph because the males possess the normal sexually dimorphic plumage features of the species (white-spotted chestnut flanks, black throat barring and breast band). These could have an influence on tutor choice. All the adults used in the experiments were chosen as showing normal behaviour and typical songs for the species. They had either been reared in the laboratory or were obtained from local breeders.

All birds had constant access to a foreign finch seed mixture, cuttlefish bone and drinking and bathing water. Adults with chicks were given an egg-biscuit mixture daily, and lettuce was provided once a week. Hay was provided for nest-building when necessary. Artificial lighting ensured that the day length that birds were exposed to never dropped below 14 hours. The temperature in the birdroom was maintained at 20-25^{o}C.

PROCEDURE

Experiment 1: Young birds were reared by foster parents, in pairs of the same colour, up to 35 days of age. They were then

Figure 2.1 Grey morph (wild-type) zebra finches

Female - left. Male - right.

Figure 2.2 Chestnut-flanked white zebra finches

Not ready yet.

exposed simultaneously to two males, one of each morph, until 100 days. In this period double cages were used, with the brood of juveniles separated by a wire mesh partition from the two tutors to reduce the chance of the results being affected by different levels of physical interaction with the young. Throughout the experiment, other individuals in the birdroom could be heard and seen (though always at more than 3m range).

The experiment used a total of 22 males from 10 broods: 5 of these broods contained siblings of both morphs, while the young in the remainder were all alike but cross-fostered to a pair of the alternative colour. There was no evidence that the results of birds from mixed broods differed from those in broods of a single morph, so they have been combined for analysis.

Experiment 2: The young here were housed with their parents until 35 days and then exposed sequentially to two tutors, the first (T_1) of the non-parental morph (from 35 to 65 days) and the second (T_2) of the parental morph (from 65 to 100 days). Again during these tutoring periods the juveniles were kept in one half of a double cage, separated by a mesh partition from the adult male. As with the previous experiment, individuals within a brood were kept together as a unit, and the young were in broods of both mixed and single morphs, but no effect of this was detected. Altogether the experiment used 26 males taken from 14 broods.

In the schedule used for this experiment, we would expect from earlier studies (reviewed by Slater et al 1988) a preference for the tutor experienced from 35 to 65 days. However, the

tutor sequence used in these earlier experiments was not identical to the present one, there being a 10 day gap in tutoring from 70 to 80 days, for example (Clayton 1987c). We therefore ran a group of controls, in which the adults were all of the same morph, without this gap and with the switch in tutors at 65 days rather than 70 to match the present experiment.

Experiment 3: The young were housed with their parents (both of a single morph) up to 35, 50 or 65 days, and were then switched to the company of a tutor of the alternative morph, behind a mesh partition, until 100 days. Results were compared to those of Eales (1985b), who used the same regime but without the change in colour morph.

After 100 days, juveniles from all three experiments were kept together in their separate broods, in single cages within the birdroom, until their songs had been recorded and they had been tested for mate choice. This experiment involved 46 males from 25 broods.

Mate choice testing: All young males were given at least two half-hour preference tests. Each of these consisted of the presentation of two females, one of each morph, on either side of the male in a triple cage split with mesh dividers. Females used as models for a particular male had been reared by parents of his morph to equate as far as possible the likelihood that the two females would respond to him. Different pairs of females were used in each test for a given male.

The birds were given five minutes to settle down before the test. The number of phrases of directed song sung to each female over the half hour was then recorded. If birds of the same colour received the most song in two tests, then the male was scored as having a preference for that morph. A further test, with a third pair of females, was carried out if the first two tests gave opposite results. One bird did not sing at all in three tests, so no mate preference was recorded for him.

These tests were carried out in a room in which there were no other birds and all of them took place between 0900 and 1600 hrs GMT.

Song tutor choice: The songs of all birds were recorded with a Uher 4000 tape recorder and were sonagrammed using a Kay Digital sonagraph 7800. Determination of song tutor choice was achieved by comparing the sonagrams by eye. Individual elements within the song phrase of young males were scored, where possible, as having been copied from the father or from one of the tutors. In some cases, however, there was either no close match at all (these elements were probably either improvised or copied from birds elsewhere in the birdroom), or it was impossible to distinguish between an element possessed by more than one of the adults.

The preferred song tutor of each juvenile male was determined. This was the tutor whose elements contributed the most to the young bird's song. If elements from two of the adults were represented equally, then the bird was scored as having no preferred tutor. Thus the sample sizes quoted in the Figures

are often lower than the total numbers of birds used in an experiment given above. Although occasional mistakes in the allocating of elements probably occurred where those of two tutors were similar, this would not have had a strong effect on the results. In nearly all cases, one tutor was clearly preferred to the others. The mean number of elements/song of all young birds in the study (n=94) was 9.45 (S.D.= 2.55), and of these a mean of 6.42 (S.D.= 2.79) were derived from the preferred tutor, 1.37 (S.D.= 1.47) were from other males and 1.66 (S.D.= 1.70) were of uncertain origin.

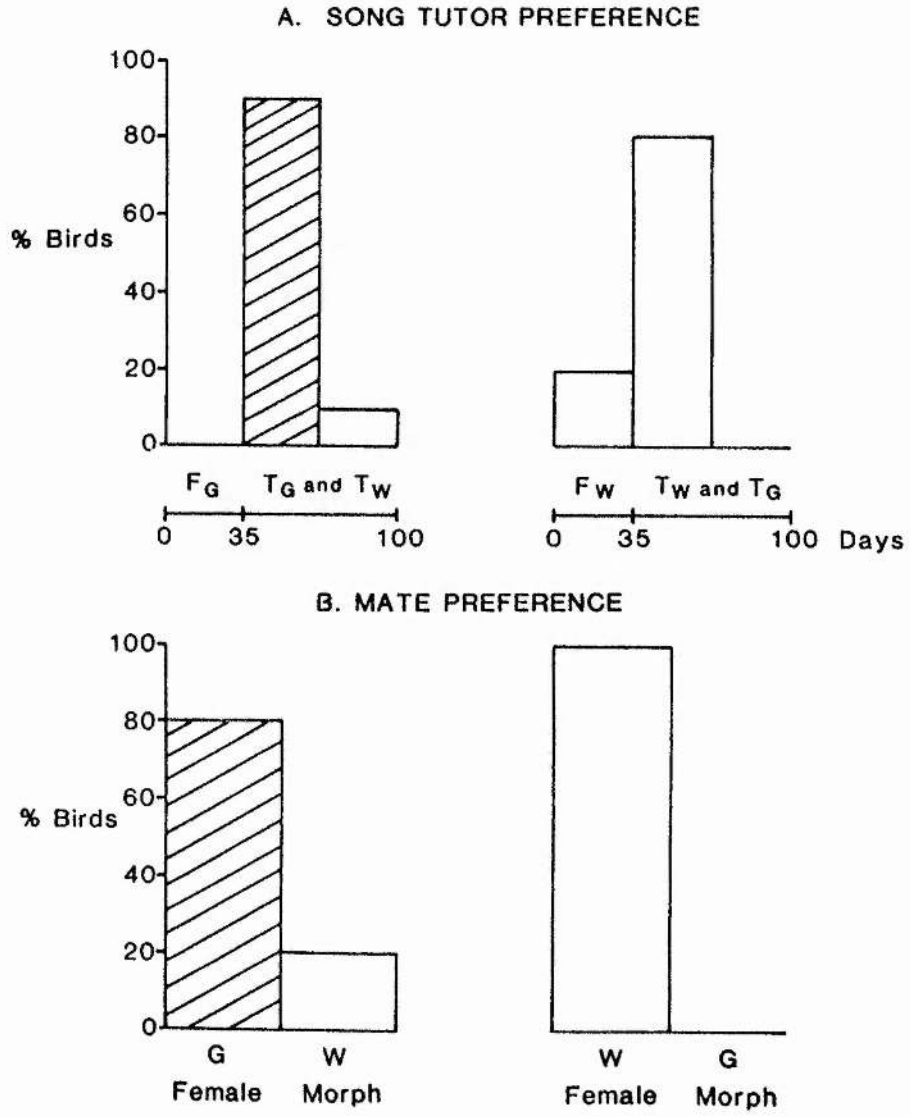
2.3 Results

Experiment 1: Simultaneous Exposure to Tutors of Two Morphs

a) Song learning

Nine out of ten males with grey parents selected the tutor of that colour as the preferred song model (Sign test, one-tailed, $p = 0.011$), while eight of the twelve males with white parents chose the white tutor ($p = 0.19$; combined results from the two morphs, $p = 0.008$) (Figure 2.3a). Of the remaining five birds, two copied most from their father, and two copied equally from the father and the other bird of his morph. Only one young bird out of the 22 in the experiment showed most learning from the tutor that was not of the parental morph. There was no evidence that young birds preferred to learn from one morph rather than the other (for example, showing a preference for wild-type tutors) irrespective of parent-type (9 preferred grey and 11 preferred white).

Figure 2.3. The song and mate preferences of young birds exposed to both grey and white males from 35-100 days. n=10 in all histograms. Open column, white preferred; hatched column, grey preferred. F_G, Father grey; F_W, Father white; T_G, Tutor grey; T_W, Tutor white.



b) Mate preference

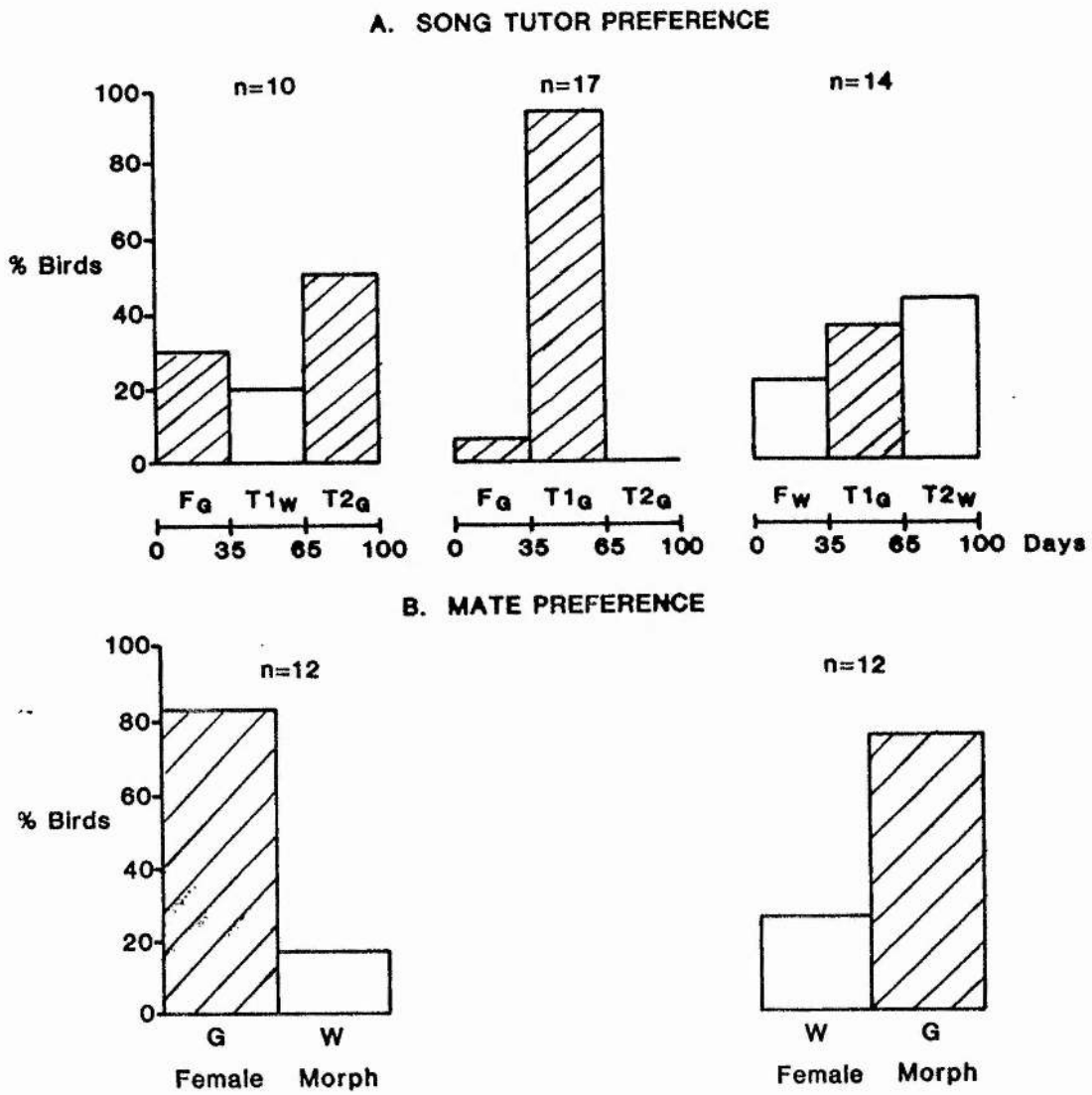
Eight out of the ten males with grey parents showed a mate preference for grey females (Sign test, $p = 0.055$) while all twelve males with white parents preferred white females ($p < 0.003$; overall, $p < 0.001$) (Figure 2.3b). Again, there was no evidence that whether the parents were actually grey or white influenced the preference.

Experiment 2: Sequential Exposure to Tutors of Two Morphs

a) Song learning

The controls, in which young birds were exposed to three different males of the same morph in succession, confirmed the earlier results: 16/17 of the young males copied most from T_1, the tutor they were exposed to from 35 to 65 days. The preference for learning from this tutor is considerably reduced if it is not of the parental morph (Figure 2.4a). Only 2/10 birds with grey parents learnt most from this bird ($X^2 = 15.57$, d.f.= 1, $p < 0.001$). Three learnt most from the father, and five from the bird experienced after 65 days. For birds with white parents 5/14 learnt most in the 35-65 day period ($X^2 = 11.98$, $p < 0.001$), with three of the remaining birds learning earlier and six later. As in Experiment 1, the pattern of results was similar whether the parents were grey or white. Combining the results for the two colour morphs, the song learning pattern where there was a switch in morph differed significantly from that where all the adults used were grey ($X^2 = 17.05$, $p < 0.001$).

Figure 2.4. The song and mate preferences of young birds exposed to two tutors in succession from 35-100 days. Other conventions as for Fig. 2.3.



b) Mate preference

In contrast to the results of Experiment 1, grey females were preferred as mates irrespective of the morph of the parents (Figure 2.4b). Overall, 13/24 birds preferred the morph of their parents (Sign test, $p > 0.5$), whereas 19/24 preferred the grey female ($p < 0.003$).

Experiment 3: Varying the Length of Exposure to the Father

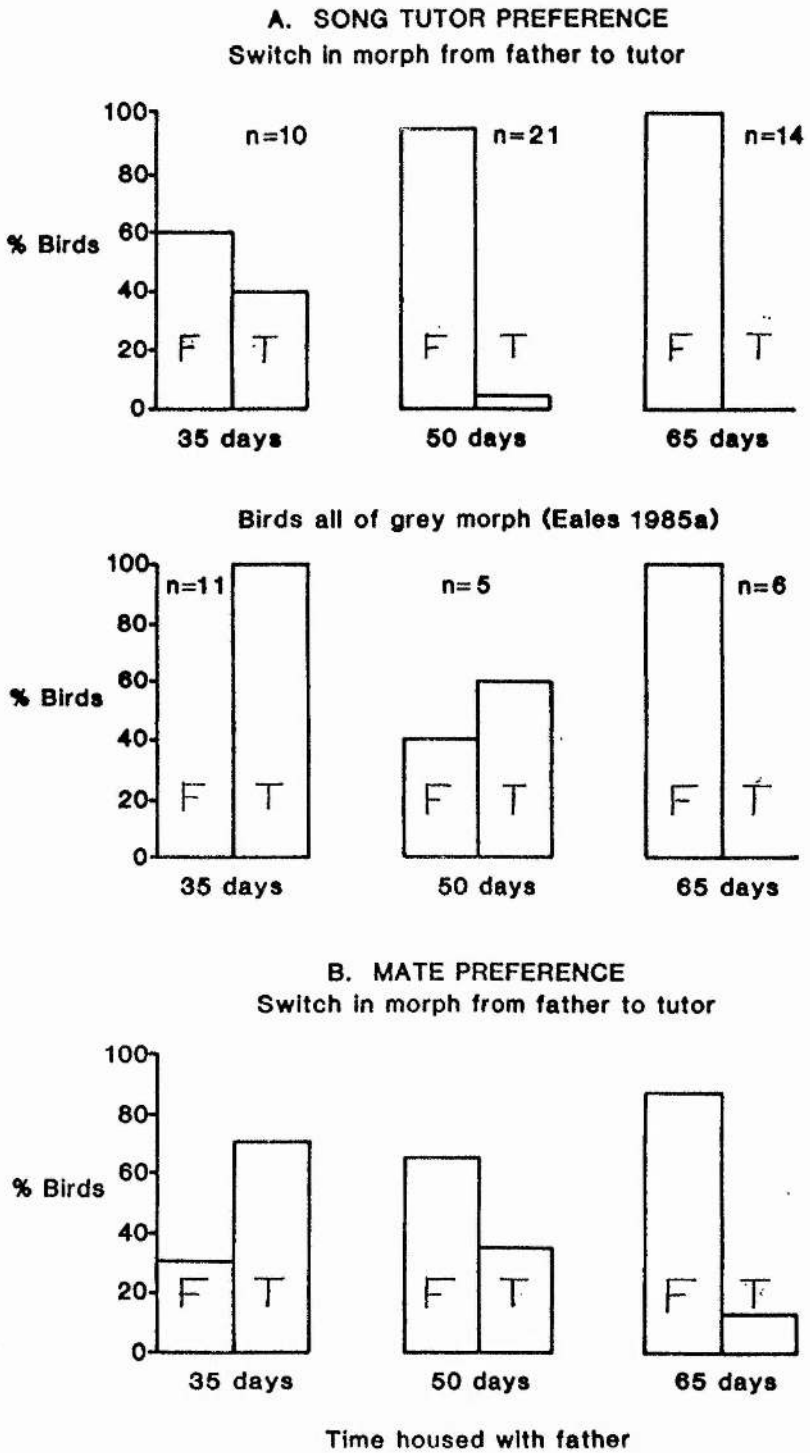
a) Song learning

The results of the song preference analysis were compared to those reported by Eales (1985b), who used an identical experimental design but without the switch in morph from parents to tutor. There is a clear difference between the two studies (Figure 2.5a). Six out of 10 birds transferred to a tutor of a different colour at 35 days showed most learning from the father. Eales, using grey birds only, found that all learning was from the tutor they experienced after the switch.

With a 50 day switch, 20 out of 21 males produced songs based mainly on those of their fathers where there was a change in morph, whereas Eales found that 3 out of 5 still chose the song of the tutor where there was no morph change (Fisher exact test, $p < 0.05$). A switch from father to tutor at 65 days resulted in the production of only the fathers' songs, in both studies.

In the present experiment, there was no suggestion that the results were affected by whether the parents were white or grey in the 50 and 65 day groups, as the results of these were very

Figure 2.5. The song and mate preferences of young birds moved from the company of their father to that of a male of the alternative morph at 35, 50 and 65 days. Control data on song tutor preferences in centre histogram are from experiments where both males were grey carried out by Eales (1985b).



uniform. There was a bias in the group moved at 35 days towards birds with white parents learning from the father (5/6), and those with grey ones learning from the tutor (3/4), but the sample size is too small for any firm conclusion.

b) Mate preference

A sexual preference for females of the parental morph increases with length of exposure to the parents as shown in Figure 2.5b. The preference for the parental morph was not affected by the colour of the parents: in the experiment as a whole, 18/25 birds with white parents preferred a mate of that morph, and 11/20 of those with grey preferred grey (X^2 = 1.42, d.f.= 1, $p > 0.2$).

Comparison of Mate Preference with Song Tutor Preference

The results from Experiment 3 show a weaker preference for the parental morph in mate choice than in song tutor choice (Figure 2.5b). This difference is significant in the case of the 50-day switch from parents to tutor (X^2 = 5.96, d.f.= 1, $p < 0.02$). There is a tendency in the same direction in the other groups, but data are fewer for these and the strong effect on both measures in the 65 day group would make any difference hard to demonstrate. This is also true of Experiment 1, where the preference for the colour of the parents was very high in both measures. However, in Experiment 2, there is a similar tendency towards there being a weaker preference for the parental morph in mate choice (13/24), than in song tutor selection (17/24), although this is not significant (X^2 = 1.42, d.f.= 1, n.s.).

While the great majority of birds in these experiments preferred the same morph in mate choice tests as that from which they had learnt their songs, this was not the case for all of them. Summing results from all the experiments, 10 out of 47 birds showed a different morph preference for song learning from that they exhibited in mate choice tests. Taking birds which directed some song in the mate choice tests to both females, there was no suggestion that the percentage to each correlated with the proportion of their song elements acquired from the two morphs. There is thus no close quantitative relationship between the two preferences (see Appendix 2.1).

2.4 Discussion

This study has confirmed the strong influence that early experience has on both song tutor choice and mate choice in the zebra finch. Males experience the morph of their parents within the first 35 days of life and this leads most of them to select a song tutor of this colour if they are given a choice during the sensitive phase. In this situation, the song of the father is not normally the one that is copied, but they produce one that was heard after independence between 35 and 65 days, as previously found also by Eales (1985a,b) and Clayton (1987c).

Despite this well defined sensitive phase, considerable recent evidence points to the timing of song learning in zebra finches being very flexible. A young male will base his song, at least partly, on that of his father, even if this was heard only before 35 days, if later tutoring is in some way inadequate. This situation arises, for example, if visual contact with a

subsequent tutor is prohibited (Eales 1989, Böhner 1990), if the tutor is visible but some distance away (Adret, pers. comm.), or if exposure beyond 35 days is to a male Bengalese finch instead of a zebra finch (Clayton 1987c). Alternatively, increasing the contact with the father in the period before 35 days may result in his song being copied even if a suitable alternative tutor is present subsequently (Slater & Richards, 1990).

Song learning after 65 days has also been shown to be possible when birds have had restricted earlier experience. Eales (1985a,b) found that males raised by a female alone (which normally produce a very deficient song consisting mainly of female calls) will modify this by copying the song of a male they first encounter after 65 days.

The present study provides more evidence of such early and late song learning. In Experiments 2 and 3, juvenile zebra finches were exposed to a single male of an unfamiliar morph throughout the sensitive phase, and the majority of these birds recalled and sang their father's song, or produced the song of a male that they first had contact with after 65 days. With a switch from father to tutor at 50 days, almost all birds selected the song of the former. In contrast, in the study by Eales (in which only grey birds were used) the song of the second male was the most frequently chosen. This difference further demonstrates how exposure to a bird of an unfamiliar morph can affect the time course of the song learning process.

In most of these experiments some young birds are exceptions, learning either from a different morph or at a different time to others in their group. It is possible that there are simply differences between males in the timing of their sensitive phases (Eales 1985a,b), or that some birds mature more slowly and are not fully imprinted on their parents by 35 days, thus increasing the likelihood of a preference being developed for a tutor of the alternative morph. However, the most likely reason for such exceptions probably rests instead with the intrinsic complexity of the song learning system. It is no longer feasible to think in terms of sharply defined learning templates or critical periods guiding an animal along its developmental path. The final selection of a song tutor by a young zebra finch, must be seen as the consequence of experiencing a wide variety of external stimuli, the combined effect of which channels the preference in certain directions. The present study demonstrates that visual information can be very important in this respect. But other experiences may exert equal or greater effects, so that, for example, a male showing particularly stimulating behaviour or possessing an especially attractive song, might be copied even though he failed to match the imprinted appearance of the young male's parents.

Song learning from birds of particular morphs is clearly affected by some form of visual imprinting on the parents, within the period of dependence. There is likewise considerable evidence that mate choice in zebra finches is affected by experience at that stage (ten Cate 1982, 1984, 1986b). How similar, then, are these two processes? Are the preferences for

mates and tutors perhaps influenced by the same imprinting event?

In general terms, there are obvious parallels between the ways in which development affects mate choice and song tutor choice. The social environment in which a bird is raised has a pronounced influence on when a song is learnt and from whom, just as it does on who will be courted when sexual maturity is reached. In the present study most experiments showed a strong preference for the parental morph in mate choice as well as in song tutor choice, indicating that experience prior to 35 days is of great importance to both.

However, there are differences. Individuals did not always choose in the same way for both processes. Several birds showed clear song learning from one morph but preferred the other in mate choice tests. Clayton (1988) similarly found that males do not necessarily select song tutors of the same species as that on which they are sexually imprinted, based on experiments in which birds were raised by mixed pairs of zebra and Bengalese finches. In the present study, an interesting additional point is that birds of the non-parental colour were chosen more often as mates than as song tutors. This may suggest that sexual imprinting (at least with respect to colour morph) occurs later than the imprinting which affects song tutor choice, so that it partly extends beyond 35 days. If this was so, then sexual imprinting on the parents would have been incomplete when the switch to a novel morph occurred.

Alternatively, it is possible that a sexual preference based on early imprinting is more readily updated, or superseded, than a song tutor preference. In the mate choice tests some birds may have demonstrated an apparent preference for a bird of the inappropriate colour simply because behavioural cues were being used alongside information about the females' visual appearance and because fine discrimination at this initial stage of courtship is not crucial. In nature, any such inappropriate courtship would be abruptly curtailed due to a lack of sexual response from the target individual, and courtship might thus eventually come to be directed to birds of the relevant appearance *and* behaviour. On the other hand, in the case of song tutor choice, it is essential that the correct cues are followed from the outset as song does not normally change in adulthood.

In experiments with zebra finches raised by either zebra finch or Bengalese finch foster parents, Immelmann (1972a,b) found an own-species bias in sexual preference. The young males were more likely to develop a preference for the species that reared them if the foster parents were conspecifics. ten Cate (1982, 1986b) has also found such a bias, and has explained the effect as resulting from behavioural differences between the species; for example, zebra finch parents are more aggressive to their young, and also feed them more often than do Bengalese finches, and this may lead to stronger imprinting. It also seemed possible that the present experiments would reveal an overall preference for grey (wild type) birds above whites in both song tutor choice and mate choice, because the greys have the natural plumage and might also behave more normally. The only

suggestion of such a bias was in the mate choice tests in Experiment 2 (where there was sequential exposure to the two morphs). This situation may be one in which males are particularly prone to responding to behavioural cues, as they have experienced only one morph at a time and, in particular, there has been a break in their exposure to the parental morph. On the other hand, with the simultaneous exposure to the tutors in Experiment 1, there is no such dramatic switch, and the colour imprinting based on parental morphology may have been reinforced by their immediate subsequent experience of another bird of the same morph.

No such wild-type preferences were found in any of the song tutor choice results. This may be because, as suggested earlier, the preference for a song tutor of the parental colour is stronger than that for a mate, and therefore over-rides the effect of any differences in behaviour between the morphs. Such differences are, in any case, only a theoretical possibility at present, as the two morphs have not been studied from this viewpoint.

As a final point, Kruijt et al. (1983) showed that siblings may exert some influences on the sexual preferences of cross-fostered zebra finches. Likewise, Clayton (1987a) suggested that the own-species bias in the mate choice of broods switched to Bengalese foster parents might be partly due to imprinting on siblings. To examine such effects various broods of young in the three experiments reported here were cross-fostered to pairs of the alternative morph or individual chicks were transferred between broods. In either case, any imprinting on

the sibling morph would counteract the imprinting on the foster parents, and so would be likely to reduce the preference for the parental morph in song tutor or mate choice. However, no such effect could be detected, indicating that the effect of parental morph outweighs that of siblings in determining preferences in this situation. This may be sensitive to precise conditions: with larger sibling groups or reduced contact with parents, a sibling effect might well emerge.

Appendix 2.1 A closer look at the relationship between morph preferences for tutors and mates.

This study has shown that the morph preferred in mate-choice tests is usually that of the preferred song tutors. Even so, some birds do choose differently with respect to the two criteria.

The method of analysis employed so far is perhaps not the best for determining how closely the two preferences are linked. For each bird two overall morph preferences were scored; the preferred mate was the one to whom most song phrases were sung, while the preferred song tutor was the bird whose contribution was the greater to a young male's song. With this system it is not possible to look at graded preferences. For example, if a slight preference is exhibited in mate-choice, is this likely to be reflected in a similarly slight preference for the same colour in song-tutor choice?

To answer this sort of question, it is necessary to score the morph preferences as ratios. This was done as follows:

Mate choice - the % of song phrases directed to the grey females in the two or three tests carried out for each bird.

Song-tutor choice - the % of song elements learnt from birds of the grey morph, of all the elements that were assignable to a tutor. Three birds were excluded because less than half of the elements in their songs could be attributed to the

song tutors (thus there was a high likelihood of the data being unreliable).

A plot of mate choice against song tutor choice (Figure 2.6), using data from all experiments, produces a wide scatter, but with expected clumps at the top right and bottom left hand corners - a high proportion of birds strongly preferred the same morph (be it grey or white) for both mates and song tutors.

To test for a correlation here we must bear in mind that we are dealing with non-normal data. Therefore, an arcsine transformation was carried out, before the following statistical tests were performed (the standard procedure when using percentages). However, the data were still not fully normalised and so a certain amount of doubt must be cast on the accuracy of these results:

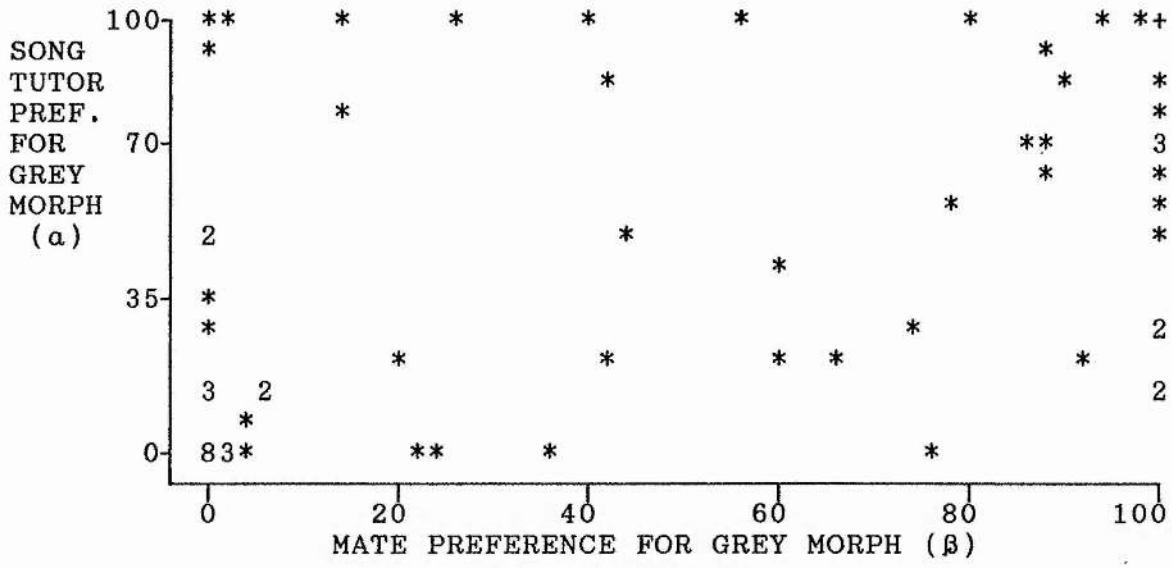
Pearson correlation of song tutor preference and mate preference: $r = 0.504$.

The regression equation is:

$$\text{s-t pref} = 0.334 + 0.469 \text{ m-c pref}$$

The gradient of the regression line (0.469) is an expression of the positive correlation between mate- and song tutor choice, and its difference from 0 is highly significant ($p < 0.001$). That there is a fair amount of scatter in the data is indicated by the fact that only 25.4% of the total variance is explained by the variance about the regression

Figure 2.6 The relationship between mate preference and song tutor preference for all birds



α - Song-tutor choice - the % of song elements learnt from birds of the grey morph.

β - Mate choice - the % of song phrases directed to grey females, in mate preference tests.

Individual birds are represented on the graph by an asterix (*). Where more than bird falls on the same point, the number of birds is entered; a cross (+) is entered where there are > 9 birds on one point.

line. However, analysis of variance shows that this represents a significant amount of the sample variance ($p < 0.001$).

The correlation indicated above is not unexpected (or particularly interesting); i.e. it does not really add anything to what we could have already surmised from the original data presentation. A strong preference for a particular morph in both mate- and song tutor choice was very likely to occur because:

i) in most cases there was a greater overall exposure to one morph, the parental, than to the other.

ii) imprinting on parental colour prior to 35 days is likely to create a strong effect anyway.

Therefore incorporating the birds that follow this strong expected pattern is of limited value, particularly as they preclude critical analysis of the preferences of the smaller number of birds that did not exhibit the "normal" pattern.

To look in more detail at whether or not a weakening of the preference for, say, the parental morph is reflected in an equivalent manner in mate- and song tutor choice, it is best to look at "ditherers". i.e. do birds that court both morphs to a substantial extent (defined here as singing between 20 and 80% of songs to grey females) also tend to show split learning from the two morphs? Is a slight favouring of one colour in mate choice reflected also in a slight favouring of that same colour in song tutor choice? A strong positive correlation, with little scatter about the regression line,

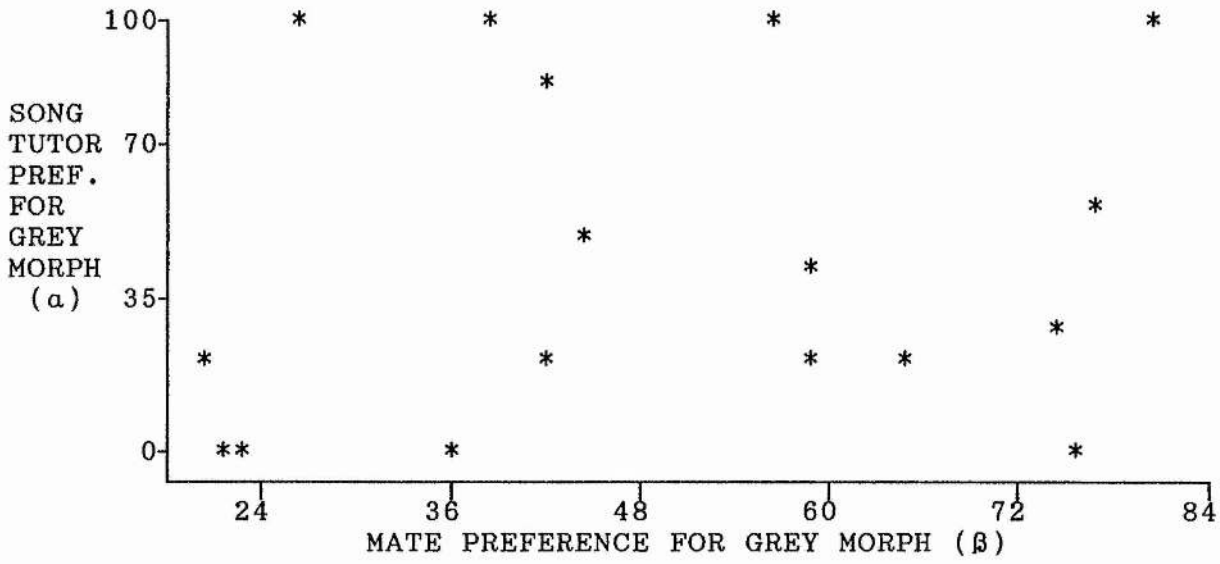
would indicate a closer linkage between mate and song tutor choice in terms of morph preference than could otherwise have been made.

The morph preferences of these "ditherers" are plotted in Figure 2.7.

There is now no hint of a correlation between song tutor and mate choice: the Pearson correlation coefficient is 0.096, and ANOVA reveals that an insignificant ($p = 0.713$) proportion of the total variance is explained by the variance about the regression line. Why? Perhaps birds that have a weaker than usual preference for mates of a particular colour are also likely to be those most easily influenced by differences in behaviour of the female models. This effectively means that only with a very large sample size might any underlying positive correlation become apparent (if it indeed exists).

In conclusion, birds do not always choose the same morph for their mates and song tutors and, furthermore, a quantitative relationship could not be found between the relative strength of the two types of preference. However, it is still not possible to make strong claims about the extent to which the two processes leading to these preferences are dissociated. This is because of the large effect that model behaviour is likely have on the results, especially for those birds that did not imprint strongly on their parents.

Figure 2.7 The relationship between mate preference and song tutor preference for "ditherers"(a)



a - "ditherers" are defined as birds that directed between 20 and 80% of their song phrases to grey females in mate choice tests.

See Figure 2.7 for explanation of symbols.

CHAPTER 3: THE INFLUENCE OF "MIXED MORPH" PARENTS ON SONG TUTOR AND MATE PREFERENCE IN ZEBRA FINCHES

3.1 Introduction

Several studies have shown that zebra finches will, under certain conditions, exhibit a preference for a song tutor, or a mate, of a particular visual appearance. Much of this work has involved cross-fostering experiments with Bengalese finches. For example, Immelmann (1969, 1972a,b) showed that cross-fostered birds tended to select individuals of their foster species as mates and song tutors, thus overriding any tendency towards species-specificity. This was the case even when conspecifics could be seen and heard during development.

However, the visual appearance of the foster-parents may have been, at most, only part of the reason for such preferences. Some birds housed in an aviary were fed by conspecifics as well as by their foster parents, and these learnt hybrid songs (Immelmann, 1969), indicating a social influence. In line with this, Eales (1987a) demonstrated that the amount of social interaction that the foster-father has with his male "offspring", affects the amount of song copied from him.

With regard to mate choice, ten Cate (1982, 1984, 1985a) argued that visual appearance, in such experiments, may be important in the development of a preference, but that a

bias may also arise due to behavioural differences. He showed that in mixed species pairs, zebra finch young are given more parental care by their conspecific parent than by the Bengalese finch parent (ten Cate 1982, 1985a), and that a correlation exists between the amount of such care and the mate preference for conspecific females (ten Cate 1984).

The influence of these differences in behaviour between species can be counteracted by performing similar experiments, but by using instead two zebra finch colour morphs. Immelmann et al (1978) raised white and grey morph birds in an aviary, with half having parents of their own colour and half the other colour. He found that both sexes directed courtship to birds of the "parental" morph, with no difference in the strength of the imprinting response between white and grey (wild-type). In Chapter 2 of this thesis, it was clearly shown that both the song tutor choice and mate choice of male zebra finches are strongly affected by visual imprinting on the plumage colour of the parents during the period of dependence (0 - 35 days after hatching).

Further evidence demonstrating an influence of plumage characters on mate preference, has come from the recent work of Clayton (e.g. 1990), on the two zebra finch subspecies. In the laboratory it was found that *castanotis* (from mainland Australia) and *guttata* (from the Lesser Sunda islands, in Indonesia) chose to mate assortatively. One of the cues that may have had a role in achieving this is male breast-band size (which is larger in *castanotis).* Increasing

the size of the breast band of *guttata* males, by painting, made such birds more attractive as mates to *castanotis* females.

The above studies show that visual exposure to the parents (or foster-parents) can influence mate preference or, in the case of males, song tutor preference. However, they do not reveal whether such preferences might be influenced by one parent more so than by the other. Are the appearances of the father and mother of equivalent importance to both male and female offspring?

In their studies of lesser snow geese, Cooke and his colleagues showed that the two colour phases, blue and white, tended to mate assortatively where both parents were alike (e.g. Cooke and McNally 1974). Where the parents were of different morphs there was no consistent preference. Also, goslings with a single male foster-parent responded in colour preference tests as clearly as those with a single female foster-parent (Mirsky 1971, in Cooke and McNally 1974). These results suggested that in this case neither parental sex was more important in determining colour preference.

Snow geese are not sexually dimorphic and, as parental duties are shared, it is perhaps not surprising that such a difference in imprinting could not be found. Zebra finch parents also provide equivalent levels of care for their offspring but, in contrast, do exhibit strong plumage differences between the sexes. It is therefore potentially

more relevant for young birds to pay particular attention to characteristics of one parent, rather than to those of the other.

Clayton (1988), reared zebra finch and Bengalese finch young with mixed parents, and then presented a choice between tutors of each species from 35 to 70 days. She found that male offspring preferred to copy songs of their own species, although a few produced hybrid songs. There was no indication of a stronger effect when the conspecific parent was of a particular sex. With regard to sexual preference, there was a non-significant tendency for males to be more directed to conspecifics where it was the mother that was of their own species. However, both parents certainly had an influence.

Again, there is a problem here of the confounding effect of using two species, with different behaviours and vocal characteristics. These factors make the search for an influence of imprinting on a particular parent more difficult: an overall bias for conspecifics could have resulted because a heterospecific parent provides a less effective imprinting stimulus, or because a heterospecific tutor acts in a less stimulating manner. Such effects could conceal an underlying pattern, whereby the parent of one sex might normally be more influential in the imprinting process than that of the other.

The present study was an investigation of the mate and song tutor preferences of zebra finches, when reared by parents

of two different colour morphs. The morphs selected were grey (wild-type) and chestnut-flanked white. Any behavioural differences between these morphs were certainly not pronounced - there was an equally strong preference for the parental morph in most of the results of Chapter 2, where the parents were both alike in colour. The only exception to this equal preference occurred in the second experiment described there, where there was sequential exposure to the two morphs. In this case, an overall mate preference for grey females resulted (it may be significant that it is under these circumstances that the influence of imprinting on the parents is likely to be weakest - see Chapter 2).

Following the same general regime as for experiment 1 (Chapter 2), a choice of two tutors, one of each morph, was given from 35 days. The following questions were of particular interest:

- would there be a mate preference for the colour morph of one sex of parent, in the case of either the male or the female offspring? If so, is it the same sex of parent that is of the most importance for both sexes?
- would male offspring have a song tutor preference for the colour morph of a specific parent (more likely the father)? If so, does this differ from that shown in mate preference tests?

3.2 Methods

Birds, housing conditions and procedure

The two morphs used in this study, grey (G) and chestnut-flanked white (W), are described in Chapter 2. The mixed-morph pairs were formed of the birds reared in experiments described there, that had been shown to have (or were likely to have) a sexual preference for a partner of the alternative morph to their own. The fathers and song tutors were all known to have normally structured songs.

The offspring of these mixed parents were reared in single cages, visually isolated from any other birds within a three metre range.

At a brood median age of 35 days, the young were taken away from their parents and rehoused in triple (three compartment) cages (Figure 3.1). The young birds were put into the centre compartment, with a single male tutor on each side, one of each morph. The design was balanced such that the grey tutor was not always on the same side of a brood. The tutors were separated from the brood by wire mesh partitions, which serve to reduce any effects of physical encounters, while still permitting song learning. Again, no other birds could be seen within three metres.

At 100 days, the young birds were rehoused in individual cages, where they were kept until they had been tested for mate preference, and until the songs of the males had been

Figure 3.1 Triple cages

These three triple cages are the type that were used in Chapters 3,4 and 6 of this thesis.

Wire mesh partitions separate the birds in the central section, from those in the outer sections.

recorded. Songs were recorded before 120 days, while mate choice testing continued up to a maximum of 150 days.

The song tutors present from 35 to 100 days were all selected on the basis that they were likely to prefer the grey morph (because of having had grey parents). It was important that they did share the same preference, because otherwise differences in tutor behaviour, and not just appearance, could have influenced the results. Grey-directed males were chosen simply because more were available. This decision should not have affected the pattern of results.

For more general details of housing, feeding and lighting, see Chapter 2.

Altogether 11 broods were involved in this experiment, five of which had a grey father and six a white father.

BEHAVIOURAL OBSERVATIONS

Ten observations, each 20 minutes in duration, were made on each cage during the period 35 to 65 days. Five were carried out in the morning, between 10.00 and 12.00, and five were in the afternoon, between 14.00 and 16.00. There were at least two days between each watch on a particular cage. Within these observations the following were recorded:
- tutor song output, and whether "undirected" or "directed" to the young birds. Total number of song phrases was also counted.

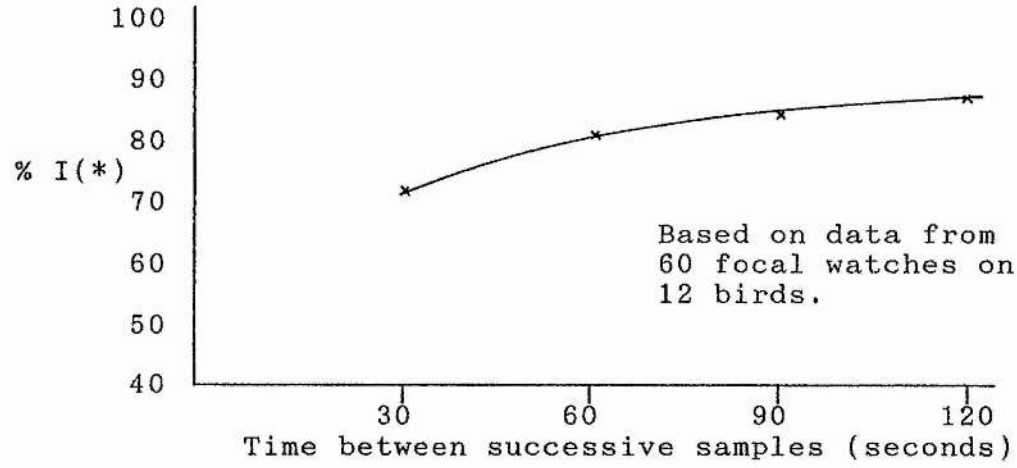
- perching positions of the juveniles. These data were collected as they might indicate a developing mate or song tutor preference. The cages of the young had two perches fitted symmetrically, and the food dish was positioned centrally. Using instantaneous sampling, it was recorded at the end of every minute whether a bird was at the side near the grey tutor, or the white tutor, or was in the middle portion of the cage. "Near" was defined as being on the nearest perch to a particular tutor, or closer, if on the floor of the cage.

The one minute sampling interval was selected as a compromise between a satisfactory level of independence between successive samples, and the requirement for collecting sufficient data from each watch (see Figure 3.2). With the chosen interval, 80.4% of successive samples had, in between, at least one change in perching location.

Song analysis

Songs of males were recorded and sonagrammed as described in Chapter 2. Analysis was done by eye. The percentage was calculated of the number of elements of a young male's song copied from each of the potential tutors, including the father. Some elements had to be left unassigned, either because a decision could not be made as to which tutor they had been copied from, or because they had apparently been improvised.

Figure 3.2 Measure of independence with differing sampling periods.



*: I = "independence". Independence in this context, in terms of a fresh choice of perching locality, is assumed where a bird changed perch position at least once between successive instantaneous samples.

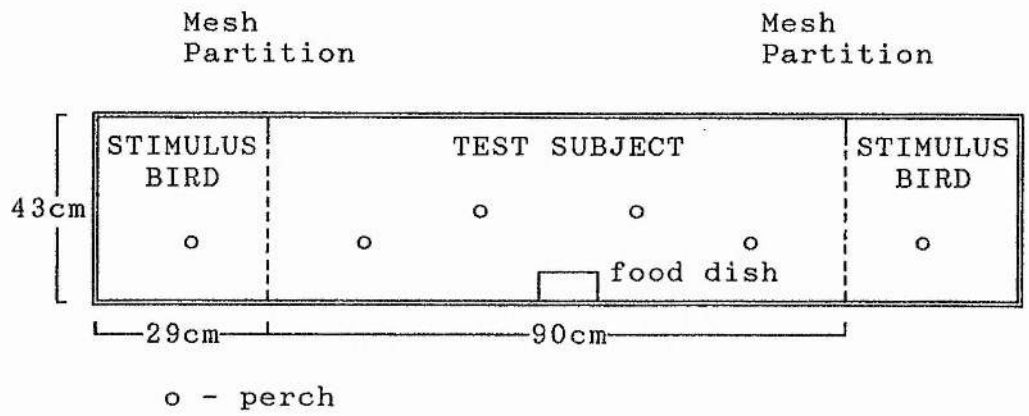
MATE CHOICE TESTING

Birds were tested for mate preference in the centre of a triple cage (Figure 3.3), with two live "models" (one of each colour morph) placed on either side, separated by wire mesh partitions. The following testing procedure was used:
1. Test bird alone in the cage for five minutes. This settling-down period allowed the individual to become accustomed to the new environment, and to recover from the disturbance of being handled.
2. Mate choice models introduced simultaneously. There was then a further delay of two minutes, again to allow time for the birds to relax.
3. Start of test.

Young males were exposed to their female models for 15 minutes, while the females were given ten minute tests. Previous studies have often used longer tests of up to 30 minutes (e.g. Clayton 1988). However, it was sometimes noticeable in the half-hour tests of Chapter 2 that young males, with an obvious initial preference for a particular female, would redirect their courtship to the alternative bird after several minutes, if the first bird did not respond. In such situations, it is apparent that a genuine preference could be concealed by longer tests.

Male offspring were judged to possess a preference for one morph above the other, if the same colour was selected in three or more out of four tests. Therefore, if the same colour was chosen in the first three tests, then a fourth

Figure 3.3 The cage used for mate preference testing



o - perch

(Cage viewed from the front)

test was not carried out. A preference in each test was based primarily on the number of song phrases directed to each of the two females. This has been shown to be a good indicator of male sexual preference (ten Cate 1984b). If no phrases were sung in a test, then the preference was based instead on the total amount of time spent in the third of the cage nearest to each model. Instantaneous sampling, with an interval of one minute, was also carried out during each test to measure the relative proximity to the two stimulus animals; the correlation between these two recording techniques was very strong (see Appendix 3.1).

No preference was scored if each morph was preferred twice over the four tests. In such situations, a preference based on the proportion of song phrases sung to each colour, combined over the four tests, was not used; this is because it is quite likely that the degree of preference shown in a single test would have been affected greatly by model behaviour.

Perching locations were also used in determining female mate preference. Perching proximity is unlikely to be as good an indicator of sexual preference as directed song, so females were given five tests, not four. Soliciting by the females was also looked for, as it would give a more direct measure of sexual interest, but it was not recorded. Oestradiol implants would have been needed to elicit such behaviour (eg. Clayton and Pröve 1989).

Variance in model behaviour could have considerably influenced the preferences shown by the test birds. To help gauge some of these possible effects, the song output of the models was recorded in the female tests, and in both sets of tests an activity score was calculated for each bird. This latter measure was simply a recording of whether a bird changed its perch position in each 15 second time interval. Such movements could involve hopping or flying to or from a perch, the floor or the wire partition.

To limit the possibility of behavioural differences occurring, only models that had been shown to have, or were likely to have, a sexual preference for the morph of the test bird were used. For example, if the test bird was a white female, then the grey and white models were selected on the basis of having been reared by white parents, or following the exhibiting of a preference for white in the mate choice tests carried out in Chapter 2.

To counteract the possible effect of a bird courting, or approaching, a test bird simply because of its location at a preferred side of the cage, the positions of the grey and white models were switched between successive tests.

All test birds were presented with different models for each test, and none had been encountered by them before.

3.3 Results

The main aim of the experiment was to examine whether young zebra finches imprint more strongly on the colour morph of a particular sex of parent. If so, such an effect might be strengthened depending on whether it was the father or the mother that was of the grey (wild-type) morph.
Unfortunately, this proved impossible to test because of the uneven sex ratios that resulted. Sixteen out of 19 surviving offspring that had a grey father turned out to be female, while 15 out of 20 offspring from white fathers were male. This difference is highly significant (chi-squared test, $df = 1$, $X^2 = 13.75$, $p < 0.001$), and is commented on briefly in the Discussion.

Song learning pattern

Table 3.1 shows a summary of the song learning results. Most of the songs were straightforward to analyse, with usually just one, or no, elements left unassigned. One bird, O156, was an exception. Three of its elements bore no relation to those of its tutors or father, and seemed instead to have been copied from O43, a tutor housed in another cage in the birdroom (Figure 3.4). In particular, element 3 is of an unusual and distinctive structure, and it seems unlikely to have been improvised (although it is similar to the "wheeze-like" notes sometimes produced by birds reared in conditions of social deprivation).

Table 3.1 Song learning pattern

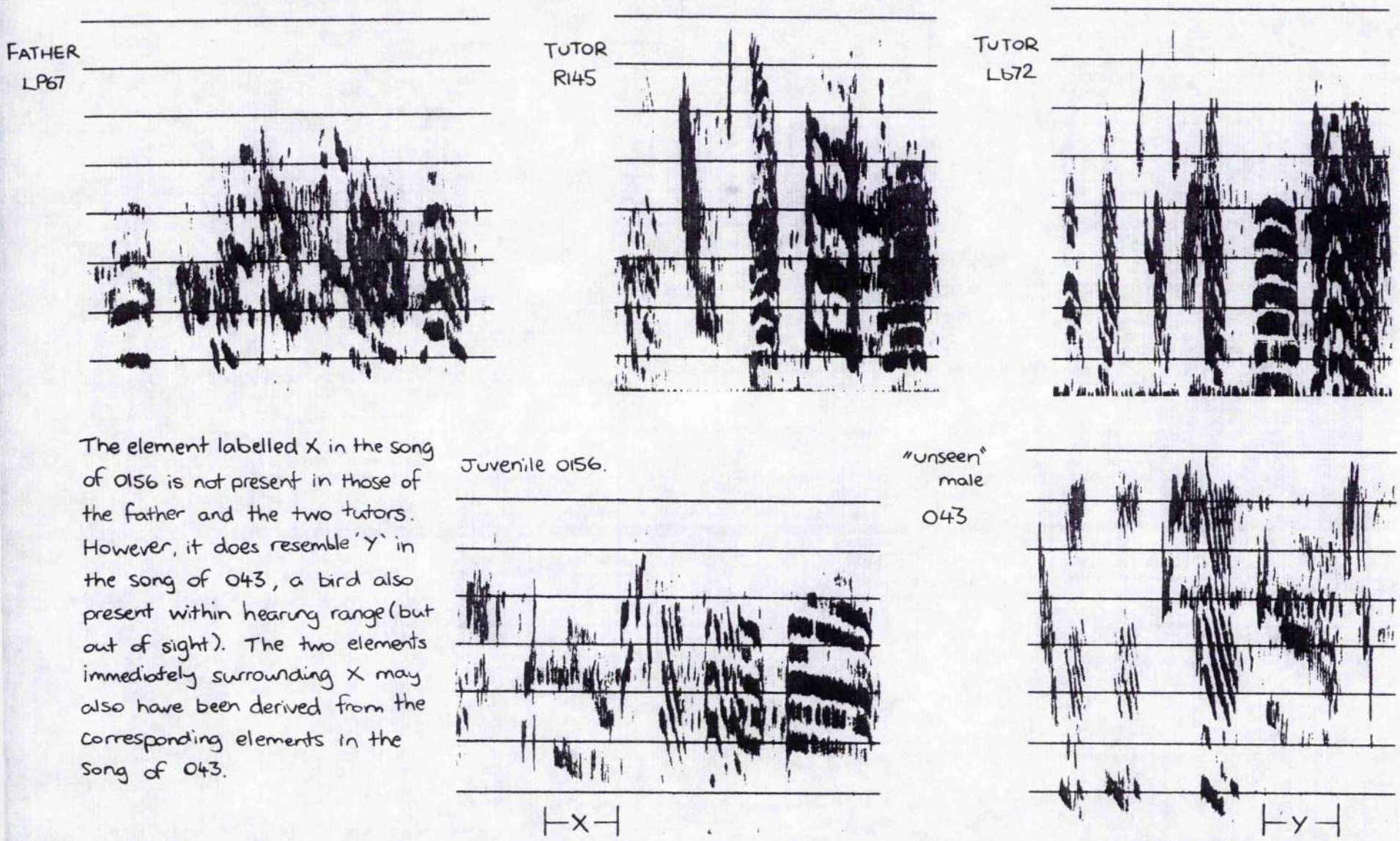
Brood	Male	Morph of Father	Source of song: Father	T_F	T_M	Unassigned
1	0151	W	0 (0)	8 (100)	0 (0)	0 (0)
	0152	W	1 (12.5)	7 (87.5)	0 (0)	0 (0)
	0153	W	0 (0)	9 (90)	0 (0)	1 (10)
2	0169	W	0 (0)	11 (100)	0 (0)	0 (0)
3	0166	G	0 (0)	9 (90)	0 (0)	1 (10)
4	0172	G	2 (25)	4 (50)	1 (12.5)	1 (12.5)
5	0178	W	0 (0)	10 (100)	0 (0)	0 (0)
	0179	W	DIED BEFORE IT COULD BE RECORDED			
6	0155	W	0 (0)	9 (100)	0 (0)	0 (0)
	0156	W	0 (0)	4 (50)	1 (12.5)	3*(37.5)
7	0181	W	0 (0)	0 (0)	9 (100)	0 (0)
	0183	W	0 (0)	0 (0)	4 (80)	1 (10)
	0184	W	0 (0)	0 (0)	7 (100)	0 (0)
9	0189	W	1 (16.7)	3 (50)	2 (33.3)	0 (0)
	0190	W	2 (25)	0 (0)	5 (62.5)	1 (12.5)
	0214	W	3 (30)	3 (30)	3 (30)	1 (10)
	0215	W	2 (28.6)	0 (0)	5 (71.4)	0 (0)
10	0233	G	0 (0)	7 (100)	0 (0)	0 (0)

T_F - Tutor of the father's morph.
T_M - Tutor of the mother's morph.
Data portrayed show both the actual number, and also the percentage (in parentheses), of elements copied from each tutor (or that were left unassigned).

(Note: Brood 8 contained no males).

* - at least one of these elements may have been copied from a tutor elsewhere in the birdroom.

FIGURE 3.4 Probable evidence of a bird copying song from a tutor that it could not see.



The element labelled X in the song of 0156 is not present in those of the father and the two tutors. However, it does resemble 'Y' in the song of 043, a bird also present within hearing range (but out of sight). The two elements immediately surrounding X may also have been derived from the corresponding elements in the song of 043.

One tutee died before its song could be recorded and another learnt equally from the father and the two tutors. Of the rest there was, as expected, a strong preference for learning from one or other of the two tutors, rather than from the father (16 learnt mostly from a tutor, none learnt mostly from the father).

Was there a preference for learning more from the tutor of the father's morph (Tf), than from the tutor of the mother's morph (Tm)? If we consider each young male as being completely independent in its tutor selection (that is, not influenced by the choice of its siblings), then the answer is "no" - 11 learnt mostly from Tf and five mostly from Tm (binomial test, two-tailed, $n = 16$, $k = 5$, $p = 0.21$). If we consider brood preferences, however, seven contained males all of which preferred Tf, one contained males all of which preferred Tm, and one contained young with differing preferences (comparing the first two groups: binomial test, two-tailed, $n = 8$, $k = 1$, $p = 0.07$). This result more strongly suggests that a preference may exist for learning from the tutor of the father's, rather than the mother's morph.

BEHAVIOURAL OBSERVATIONS, DURING THE TUTORING PHASE

There was no correlation between perching preference of the tutees and the undirected song output of the tutors, for either the males or females (Table 3.2a and b).

Table 3.2 The relationship between tutor song output and tutor-tutee proximity

a. Male offspring.

Brood	Male	% time spent near white tutor	% of undirected song from white tutor
1	O151	36.5	76.2
	O152	49.7	76.2
	O153	35.8	76.2
2	O169	54.1	96.9
3	O166	13.2	70.9
4	O172	80.1	37.0
5	O178	56.4	37.0
	O179	57.0	37.0
6	O155	35.9	45.7
	O156		
7	O181		
	O183	66.7	26.3
	O184		
9	O189		
	O190	44.7	16.7
	O214		
	O215		
10	O233	No data	

Pearson correlation (after arcsine transformation):
$r = -0.361$, $df = 9$, $p > 0.05$

b. Female offspring.

Brood	Male	% time spent near white tutor	% of undirected song from white tutor
2	O168	58.0	96.9
3	O164		
	O165	34.9	70.9
	O167		
4	O174	65.2	37.0
4	O170	52.2	37.0
	O171		
5	O180	48.1	37.0
6	O154	54.6	45.7
7	O182	59.1	26.3
8	O185	59.1	82.0
8	O186	62.1	82.0
	O187		
9	O216	38.8	16.7
10	O217		
	O218	68.1	86.0
	O219		
11	O235	28.8	18.8

Pearson correlation (after arcsine transformation):
$r = 0.473$, $df = 10$, $p > 0.05$

Note: Combined proximities used for siblings, in cases where they could not be individually identified during the tutoring phase.

It is possible that a correlation across all birds was not found between song output and perching preference, because a preference might only be exhibited should the difference in song output be pronounced. If we consider perching preferences only in cages where song output differences between tutors proved significant across all watches (using Wilcoxon matched pairs tests), we find that there was a slight tendency to perch nearer to the bird with the highest song output (Table 3.3), although this was not significant.

Female perching preference might well be correlated more with the amount of directed (courtship), song of the tutors. However, only in two out of nine cases did females more often perch near the tutor singing the most directed song.

Looking across all broods there was no tendency for the preferred song tutor to be the one with the highest song output (Table 3.4a & b). Similarly there was no relationship between the amount of time spent perching near to a tutor and the amount of song copied from him (Table 3.5a & b).

For males and females there was no overall preference for perching nearest either the grey or the white tutor (Table 3.6), or for perching nearest the tutor of the mother's or the father's morph (Table 3.7).

MATE PREFERENCE TESTS

There was a significant correlation between the females that the male subjects sang to and the perching preferences of

Table 3.3 Perching preferences, where there were significant differences in tutor song output.

Perching preference for the tutor with the highest song output, where:

SIGNIFICANT difference in song output (*)	NON-SIGNIFICANT difference in song output
49.7	13.2
36.5	34.9 c
35.8	34.8
54.1	47.8 c
58.0	19.9
67.8 c	43.6
71.2	43.0
33.3 c	51.9
40.9	64.1 c
55.3 c	45.4
61.3	62.1 c
	59.1
	56.1 c
Median = 54.1	Median = 45.4

Mann-Whitney U test: U = 153, m = 11, n = 13, p = 0.38.

Perching preference - % of time spent close to tutor.

Percentages are for separate individuals in most cases (males or females). However, those marked c represent an overall percentage for combinations of siblings, where birds were not individually identified.

* - differences in song output between each tutor pair tested for significance using Wilcoxon matched pairs tests.

Table 3.4 The relationship between tutor song output and song tutor choice by the juvenile males.

a.

Brood	Song output (phrases/hour) of: Preferred tutor (*)	Non-preferred tutor
1	221.8	69.3
2	194.5	6.2
3	46.4	113.2
4	89.2	52.4
5	47.8	81.8
6	198.8	236.6
7	123.8	44.2
9	295.3	59.0
11	180.3	41.7

Wilcoxon matched pairs test: n = 9, W = 37, p = 0.097.

* - if more than one male within a brood, the brood preference was based on the mean number of elements copied from each tutor.

b.

Brood	Percentage of song copied from T_F (*)	Song output of T_F, as % of that sung by both tutors
1	92.5	76.2
2	100	96.9
3	90	29.1
4	50	63.0
5	100	37.0
6	75	45.7
7	0	26.3
9	20	16.7
11	100	63.0

Pearson correlation:
r = 0.572, df = 7, p = 0.108

* - where more than one male sibling, mean percentage/brood calculated. T_F - tutor of father's morph.

Table 3.5 Relationship between perching preference for a particular tutor and song tutor choice

a.

Juv. male	% perching preference for T_F	% song copied from T_F
O151	36.5	100
O152	49.7	87.5
O153	35.8	90
O169	54.1	100
O166	86.8	90
O172	19.9	50
O178	56.4	100
O155		100
O156	35.9	50
O181		0
O183	66.7	0
O184		0
O189		50
O190	44.7	0
O214		30
O215		0
O233	67.8*	100

Pearson correlation (after arcsine transformation):
r = -0.101, df = 9, p = 0.911.

* - this was a combined preference of the male with two female siblings. It was included because no differences had been found between the perching preferences of males and females. Combined preferences were also used for three groups of male siblings in the above table.

b. A simpler way of looking at this:

Birds whose song tutor preference coincided with their perching preference.	6	(Binomial test: $p > 0.05$)
Birds whose song tutor preference did not coincide with their perching preference.	10	

This is in the reverse direction to that expected, if degree of perching proximity is regarded as being a good indicator of song tutor choice.

Table 3.6 Was there an overall perching preference for either the grey or the white tutor?

	Juvenile	Perching preference for grey tutor	Perching preference for white tutor
MALES	O152	8.1	8.0
	O151	9.9	5.7
	O153	10.2	5.7
	O169	5.1	6.0
	O166	11.2	1.7
	O172	3.6	14.5
	O178	7.8	10.1
	O179	7.4	9.8
	O155/O156	11.6	6.5
	O181/O183/O184	4.6	9.2
	O189/O190]	8.4	6.8
	O214/O215]		
FEMALES	O168	5.0	6.9
	O164/O165/O167	8.2	4.4
	O174	5.7	10.7
	O170/O171	7.6	8.3
	O180	7.0	6.5
	O154	8.4	10.1
	O182	5.2	7.5
	O186/O187	5.3	8.7
	O185	5.4	7.8
	O214	9.8	6.2
	O217/O218/O219	5.0	6.4
	O235	10.4	4.2

Wilcoxon matched pairs tests:

For males - $W = 30$, $n = 11$, $p = 0.82$.

For females - $W = 46$, $n = 12$, $p = 0.61$.

For males and females combined - $W = 142$, $n = 23$, $p = 0.92$.

(Perching preference scores are the mean number of instantaneous samples, over all watches, that each juvenile spent at the side of the cage nearest each of the tutors).

Table 3.7 Was there an overall perching preference for the tutor of either the mother's (Tm) or the father's (Tf) morph?

	Juvenile	Perching preference for T_F	Perching preference for T_M
MALES	O152	8.0	8.1
	O151	5.7	9.9
	O153	5.7	10.2
	O169	6.0	5.1
	O166	11.2	1.7
	O172	3.6	14.5
	O178	10.1	7.8
	O179	9.8	7.4
	O155/O156	6.5	11.6
	O181/O183/O184	9.2	4.6
	O189/O190	6.8	8.4
	O214/O215		
FEMALES	O168	6.9	5.0
	O164/O165/O167	8.2	4.4
	O174	5.7	10.7
	O170/O171	7.6	8.3
	O180	6.5	7.0
	O154	10.1	8.4
	O182	7.5	5.2
	O186/O187	5.3	8.7
	O185	5.4	7.8
	O214	6.2	9.8
	O217/O218/O219	5.0	6.4
	O235	10.4	4.2

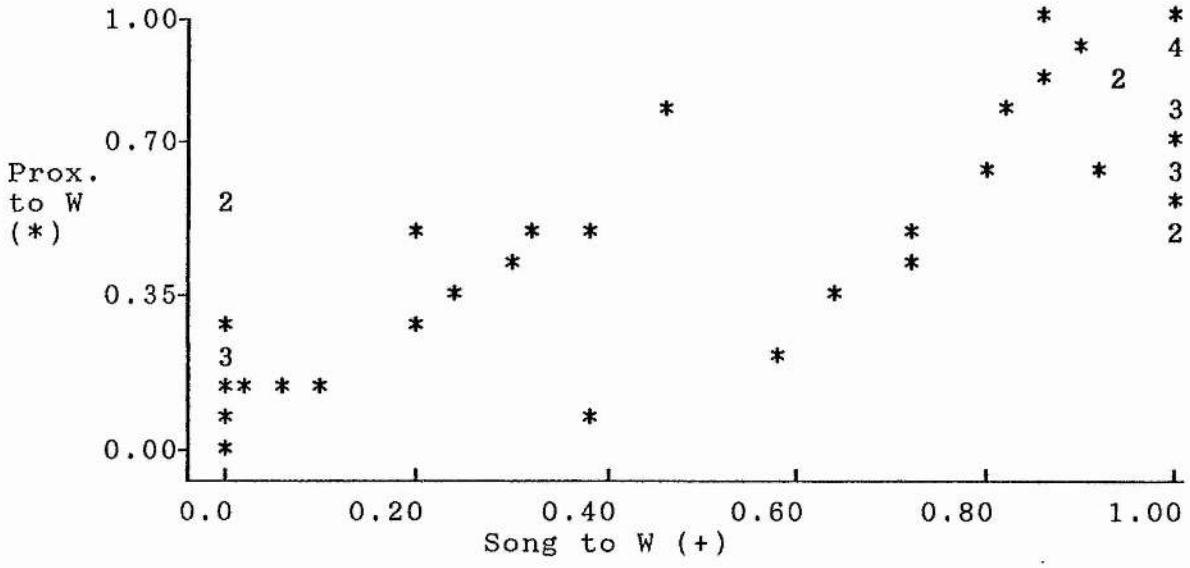
Wilcoxon matched pairs tests:

For males - $W = 29$, $n = 11$, $p = 0.76$.

For females - $W = 37$, $n = 12$, $p = 0.91$.

For males and females combined - $W = 126$, $n = 23$, $p = 0.72$.

Figure 3.5 The relationship in mate choice tests between perching proximity and directed song



* - proportion of time spent within close proximity of white females.

+ - proportion of song directed to white females.

Regression of above (after arcsine transformation), gives the probability of the gradient being 0 as $p < 0.001$. ie. there is a highly significant correlation between the objects of directed song and the perch preference, of the males that were mate-choice tested.

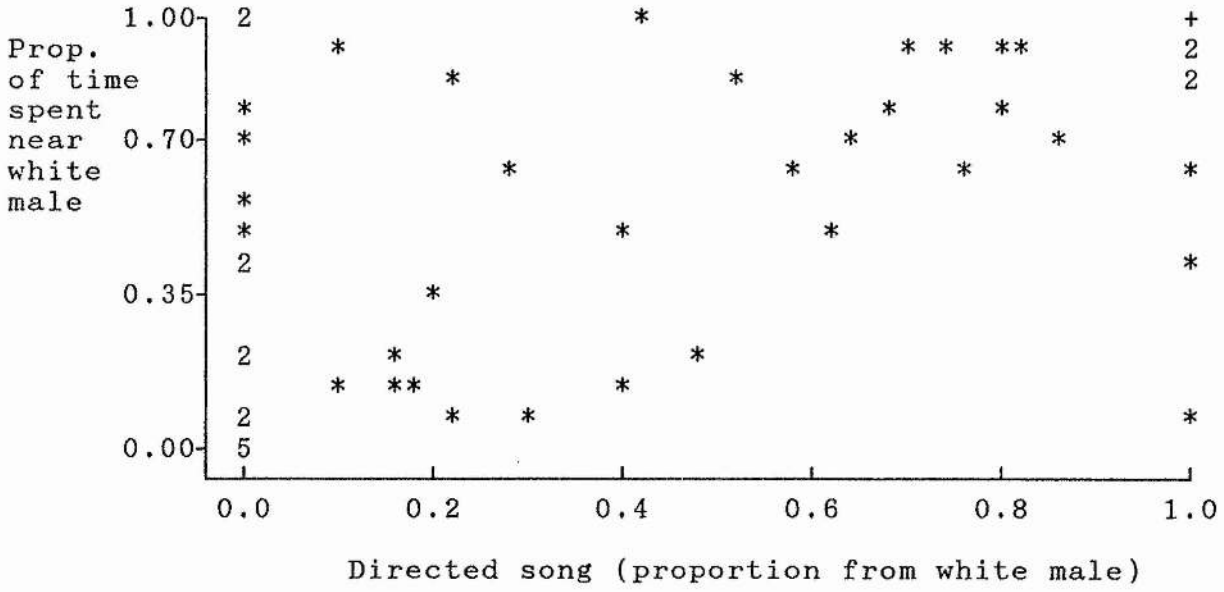
these males (Figure 3.5). In 39 of the 46 tests contributing to this result, the young males spent more of their time in close proximity to the female that they directed most of their song to. The seven exceptions were all males that sang very little during their tests, so perhaps less reliance can be placed on their supposed mate preference. The result here justifies to some extent the use of perching preference as a measure of sexual attraction, in the tests where the male did not sing, and in the tests on females (see also Discussion).

Within the mate choice tests on the male offspring, there was no relationship between the amount of song directed to the female models, and the activity scores of the latter (Pearson correlation, after arcsine transformation, $r = 0.151$, $df = 44$, $p > 0.05$). Altogether, there were 22 cases of birds singing most to the more active female, and 24 cases of more singing to the least active.

Similarly, in the female tests there was no correlation between perching preference and the activity of the male models ($r < 0.001$, $df = 83$, $p > 0.9$), but the amount of directed song of the models *was* correlated with perching preference (Figure 3.6). Under the circumstances of the mate choice tests on the females, undirected song was rare, and did not correlate with their perching preference ($r = -0.057$, $df = 13$).

The result of the mate choice tests for the males are shown in Table 3.8 and for the females in Table 3.9. Of the 13

Figure 3.6 The relationship between perching preference of the juvenile females, and the amount of directed song of the males models



Gradient of regression line (after arcsine transformation) is significantly different than 0 ($p < 0.001$).

Table 3.8 Mate preference results for males

Brood	Bird	Morph of father	Mate preference (*)
1	O151	W	G
	O152	W	?
	O153	W	Gx
2	O169	W	G
4	O172	G	W
5	O178	W	?
	O179	W	?x
6	O155	W	G
	O156	W	W
7	O181	W	G
	O183	W	W
9	O189	W	W
	O190	W	W
	O214	W	W
	O215	W	W
10	O233	G	W

No results were obtained for O166 and O184, because the birds died before completion of their mate choice testing.

* - for the criteria on which this was based, see Methods. Two birds, marked 'x', did not sing during the mate choice testing.

Table 3.9 Mate preference results for females

Brood	Bird	Morph of father	Mate preference (*)
2	O168	W	G 3
3	O164	G	W 3
	O165	G	W 3
	O167	G	W 3
4	O170	G	W 3
	O171	G	G 3
	O174	G	W 3
5	O180	W	W 3
6	O154	W	G 3
7	O182	W	G 3
8	O185	G	W 4
	O186	G	W 5
	O187	G	W 3
9	O216	W	G 3
10	O217	G	G 4
	O218	G	W 3
	O219	G	W 4
11	O232	G	G 4
	O235	G	W 5

No results were obtained for O231, because this bird died before it could be mate choice tested.

* - for the criteria on which this was based, see Methods. The number of tests (out of five) in which birds perched closer to their "preferred" morph, is given following the morph preference.

males that showed a preference over the four tests (following the definition of preference given in the Methods), seven preferred the mother's morph and six the father's morph. If brood preferences are looked at, four contained young all preferring the mother, one contained young all preferring the father, and three contained young that differed in their preferences (or that had no preference).

Of the females, four preferred the morph of the father and 15 the morph of the mother (binomial test, two-tailed, $n = 19$, $k = 4$, $p = 0.01$). Again, if we consider broods as a whole, six contained female offspring showing a preference only for the mother's morph, with one "brood" selecting the father's morph and with three showing a split preference.

Male and female offspring did not differ significantly in their morph preference in the mate choice tests (Table 3.10). Combining the data from both sexes, there was a mate preference for the mother's colour morph, which was just significant (binomial test, two-tailed, $n = 32$, $k = 10$, $p = 0.05$).

Males did not show a significant difference in their degree of preference for the father's or mother's morph, when song tutor or mate choice were compared (Table 3.11), using data from individuals that demonstrated a preference on both criteria. Despite this, only three out of 12 birds preferred the same morph both as their song tutor and as their mate. If the results from the mate choice testing are separated

Table 3.10 Did male and female offspring show a difference in morph preference?

	Mate preference for: Father's morph	Mother's morph
Males	6	7
Females	4	15

Fisher Exact Test: $p = 0.13$

Table 3.11 Comparison of song tutor and mate preference of the juvenile males

		Mate preference for: Father's morph	Mother's morph
Song tutor pref.	Father's morph	2	6
	Mother's morph	3	1

Fisher Exact Test: $p = 0.15$

Table 3.12 Relative mate and song tutor preference for the morph of the father, with the choices made by each individual being treated independently

	Preferred morph: That of father	That of mother
Song tutor preference	11	5
Mate preference	6	7

Chi-squared = 1.51, df = 1, $0.2 < p < 0.3$

from the song tutor preferences, there is an indication that the father's morph might be more influential in the latter than the former. This effect is not significant with data analysed at the level of the individual (Table 3.12); however, if broods showing a consistent preference are used as the unit of analysis, the effect does reach significance (song tutor preference - 7/8 broods preferred the father's morph; mate preference - 1/5 broods preferred the father's morph: Fisher exact test, $p = 0.032$).

3.4 Discussion

Walter (1973) concluded from a series of experiments, which involved the exposure of zebra finches to "pure" white or grey (wild-type) parents, that males develop a sexual preference for the colour morph of their parents, whereas females always prefer grey. Where parents were of mixed morph (the father grey, the mother white), the mate preference of males was apparently random with regard to colour. She suggested that this implies that imprinting is "independent of the colour of a particular parent but occurs randomly to the general colour of one parent."

Females with a grey father and white mother again preferred grey mates. Walter argued that this consistent grey preference is evidence that females do not imprint (particularly as birds with white parents preferred grey, despite never having previously experienced a grey male).

HOW DO THE PRESENT RESULTS COMPARE WITH THE ABOVE FINDINGS?

1. Were male preferences influenced by both parents?

In this study six out of 13 males preferred females of the father's morph, in the mate choice tests. In experiment 1 of Chapter 2, where the only important difference in design was that both parents were of the same colour, 20 out of 22 males preferred the father's morph (comparison of the relative preferences for the father: Fisher exact test, $p = 0.006$). This shows, in agreement with Walter, and also with Clayton (1988), that early experience with both parents can influence a male's mate preference.

The song tutor preference of the experimental males was similar, with the father's morph being more strongly selected when both parents were alike in colour (Chapter 2, 21/22 copied mainly from F; present study, 11/16 copied mainly from F: Fisher exact test, $p = 0.038$).

2. Do males choose their mates randomly, in relation to the colour morphs of their father and mother?

Again in agreement with Walter, males did not show a general mate preference for either the colour of the father or of the mother.

3. Do females imprint?

There was no overall preference for grey males (seven preferred grey, 12 preferred white). This is in agreement with a study by Sonnemann and Sjölander (1977), which showed clearly that early experience, in their case with Bengalese finch foster parents, can influence the later mate choice of female zebra finches. It is, however, in sharp contrast to Walter's results, where 6/6 preferred grey when the parents were mixed, and where 17/18 preferred grey when the parents were both white. In the present experiment females showed a significant mate preference for the mother's morph.

The first possible reason that might explain why only Walter's birds strongly preferred grey, relates to the behaviour of the male models. Her grey males were wild-caught, or the progeny of such wild birds, whereas her white males were highly domesticated. Significant behavioural differences may therefore have existed between the two colours. This may be particularly relevant in her case because pure white zebra finches have been described as having "some serious disturbances" in their courtship behaviour (Martin 1984). It is well established that female sexual preferences can be greatly influenced by variance in male behaviour (for example, correlations between female preference and male courtship criteria have been shown by work on mallards by Bossema and Kruijt 1982, and by Kruijt, Bossema and Lammers 1982, and also by ten Cate and Mug 1984, working on zebra finches). The two morphs in the present study are perhaps less likely to have had differing

behaviour, as both (even those of the wild-type) were from thoroughly domesticated stock.

If we make the assumption, based on this study and on that of Sonnemann and Sjölander (1977), that females do indeed imprint on their parents early in life, we can suggest another reason for the difference in the results. Where they had mixed-morph parents, Walter's young birds may have imprinted on the sexually dimorphic plumage characteristics of male zebra finches (cheek patches, breast band and flank markings) in their first 28 days of life. Then, when presented with a choice of a white or a grey mate at adulthood, they avoided the former because, lacking such characteristics (the "pure" white morph male has a redder bill than the female, but otherwise looks alike), it provided a weaker stimulus. There might even have been a strong aversion to this white bird, because it effectively displayed a mixture of a female's appearance with a male's behaviour (as far as the previous experience of the test birds was concerned).

However, there is a problem with such conclusions, when Walter's results from the birds with two white parents are considered. If later preference was based purely on early experience with particular colour morphs, then these females should have been more attracted to the white test bird, than the grey male which had different ground colour and the presence of the unfamiliar sexually dimorphic features. Again, perhaps there was a strong, over-riding preference for the grey males because of a behavioural difference. The

alternative to this must now be that females had a preference for males possessing the sexually dimorphic characteristics, regardless of early experience. This could be tested by presenting female-raised zebra finches with a choice of two white males, one with and one without the specific male plumage traits.

In the present study, even females with grey fathers preferred males of the mother's colour morph as mates. As the father was grey in all of Walter's pairs of mixed parentage, this is the group that is most comparable. Why then, is there such a difference in results? There are three possibilities:

i) Both male models exhibited the sexually dimorphic plumage features, and not just the grey; therefore a potential bias due to a preference for birds showing these characteristics would not have occurred.

ii) In Walter's case separation from the parents occurred at 28 days, not 35 as in the present situation. The period of extended contact could have been important in the imprinting process.

iii) As mentioned previously, a bias created by behavioural differences between the morphs was less likely to have occurred.

It is difficult to answer the question "why should females have shown a sexual preference for the mother's morph?" Perhaps it was the result of greater exposure to the mother early in life, due to the type of interaction she had with her (female) offspring, but there is no evidence to support

this; ten Cate (1982) reported no differences between the two sexes of parent, in the time they spent inside the nest box, or in the number of feeding bouts that they delivered to their offspring. Functional explanations are no more obvious.

Are females less strongly affected by imprinting than males? Immelmann (1972a,b, 1975) argues that they are. According to Immelmann, females tend to have a more pronounced "own-species" or "wild-type" bias in their mate preference, and can more easily rely on unlearned characteristics because of the male being brighter, with a more elaborate courtship display. Ten Cate (1988) argues differently. He points out that sometimes females do not demonstrate a strong preference based on imprinting on their parents, because they more often use behavioural cues in addition to visual ones. In this way, underlying preferences can be overridden. The results in this chapter provide some support for this viewpoint - despite the known influences of male behaviour, there was a significant preference for the mother's morph; this suggests that female zebra finches did imprint, at least to some extent, early in life.

The over-riding pre-disposition for choosing grey mates, as suggested by Immelmann and by Walter, would now seem ungrounded. It remains possible, however, that there is an underlying preference for the sexually dimorphic features of males. This would perhaps not be surprising, as the presence of such features could well have resulted through the process of sexual selection by female choice.

Were male song tutor preferences influenced by the colour morphs of both parents? The answer to this question is "yes", even though there was a bias towards a preference for the father's morph (significantly so, compared to mate preference, if whole brood choices were considered). Males frequently displayed a different morph preference, in relation to song tutor and mate choice. This agrees with the results from Chapter 2, and could be seen as evidence for there being separate imprinting processes involved in the development of the two preferences. Alternatively, this pattern could simply be a reflection of the way in which the varying behaviour of tutors, or of female models, can obscure an underlying preference.

Why should males prefer a song tutor of the father's morph, if this is indeed the case? There are plausible functional reasons why this should be so. For example, it seems more relevant to learn the appropriate appearance of a song model from the father. (In a similar way it would make sense if the mother's appearance was followed with regard to mate-choice, but this did not happen). A causal reason behind this apparent preference for the tutor of the father's morph could be that male offspring have, during their early development, imprinted more strongly on their fathers. Such stronger imprinting may itself have been the consequence of the greater salience of the male, due perhaps to his singing or aggression.

There is a danger here of leaping to invalid conclusions concerning a general imprinting phenomenon, simply because

the data seem to fit a common-sense functional explanation. The preference for the father's morph could equally be explained by considering a young male's choice as being either for a novel or a familiar stimulus. The process of imprinting involves a developing preference for familiarity, such that novel objects are increasingly ignored or avoided (reviews by Bateson 1978b, 1987). Zebra finches might imprint equally on both the mother and the father, with the characteristics of both being stored separately (whether this is the case, or whether they are likely to be combined, has been studied by ten Cate (1986b, 1987). If they subsequently encounter two individuals, with one similar to a stored image and the other different, then it would not be surprising if the former was preferred. This could be precisely the situation in the present experiment, and equivalent to that which possibly occurred in Walter's study, where female zebra finches with mixed morph parents preferred grey mates. In this case the tutors effectively included a male that bore a close resemblance to the father, and another that looked like the mother in its ground colour, but with sexually dimorphic features. The second tutor could therefore be regarded as having a third, novel morphology and for this reason alone may have been avoided.

This problem could have been alleviated by using two morphs, neither of which were sexually dimorphic. In practice this would have proved difficult, as such birds are not readily available. Alternatively "pure" whites could have been used, marked to create artificial dimorphism (a technique being

used by Vos, in prep., to study imprinting and supernormality in zebra finches).

In addition to the morph preference shown by male zebra finches for their song tutors, was there any evidence for an influence on the preferences of the behavioural characteristics of the tutors? The relative tutor song output was close to having a significant effect; an influence in one or two cases was quite likely, where the tutor that was not selected had a very low song rate, particularly in relation to that of the other tutor.

Surprisingly, there was no indication that the preferred perching location of the tutees acted as an indicator of their tutor choice.

This study has, in summary, provided evidence that:
i) in agreement with Sonnemann and Sjölander (1977), but contrary to Walter (1973), females do imprint at least to some extent on the morphology of their parents. It remains unclear whether one parent has a greater influence, but there was a tendency towards a preference for males of the mother's morph.
ii) in mate and song tutor choice, males showed evidence of being influenced by the appearance of both parents and not just one.

Beyond this, further conclusions (for example, regarding the strength of the male preference for the father's morph) have

necessarily been tentative, because of problems with interpretation.

The problem of song tutor and mate choice models including individuals that were effectively novel, and not just representations of the mother's or father's morphology, has already been discussed.

Was it appropriate to use multiple tests, for elucidating the preference of a single individual? The answer to this is not clear. Multiple tests were used because, if behavioural influences on choice are considerable, a single test would be quite likely to produce an unrepresentative result. However, it is known that a single test of the kind used here, can greatly affect the subsequent preference displayed by the birds involved (Immelmann et al 1991, Kruijt and Meeuwissen 1991). Multiple tests could not therefore be regarded as being independent of each other. The best solution would be to have a single test in which the stimulus birds were less able to interact with the test bird, so reducing the possibility of their behaviour affecting the choice. One-way mirrors would achieve this, although for males mounted models would probably suffice, particularly if they were of females in the soliciting posture.

How appropriate was it to assess female mate preferences solely by the perching preferences that they displayed? This can be justified to some extent from previous work; ten Cate and Mug (1984) demonstrated a close relationship

between the time spent close to stimulus males and the amount of tail quivering (an overt sexual response) by the females. Also Clayton (1990), in a study on Timor and Mainland zebra finches found that perching preferences in 10-hour choice tests correlated well with later pair formation. Furthermore, male sexual preferences in the present study, measured by song output, correlated well with their perching preferences.

This last point, however, raises a potential problem. If the white males were, for some reason, more sexually motivated and sang more to female test birds than did grey males, then this might have influenced female preference. Certainly there was a good correlation between female perching proximity and the model that had the highest directed song output. It is therefore important to address the question of which is the cause and which the effect of the correlation. The impression was that a male only sang to a female when she approached close to his cage - if she moved away again, he would stop. Although this would imply that directed song did not cause close approach by a female, it remains possible that she developed a preference for a male that sang more frequently *when* she was close to him. The solution again would be to use one-way mirrors, so that the occurrence, and possible effect, of the song output of the male stimulus birds would be eliminated.

Siblings in the present study were housed together throughout. This raises two issues. Firstly, considering all the broods, only five out of the 39 juveniles were white.

The only comment that can really be made here is that any effect that this may have had was unlikely to have been great. Such a preponderance of grey birds as companions would be expected to have pushed juvenile preferences towards grey, irrespective of the colour of their parents. Despite this, there was no evidence of birds generally preferring grey over white.

Secondly, was there any evidence for siblings acting non-independently regarding their mate or song tutor choices? In fact, no "brood effect" could be found (see Appendix 3.2). However, finding no significant difference in the preferences exhibited between broods, does not prove that such an effect did not occur; it would still be advisable in future studies to control for possible sibling influences.

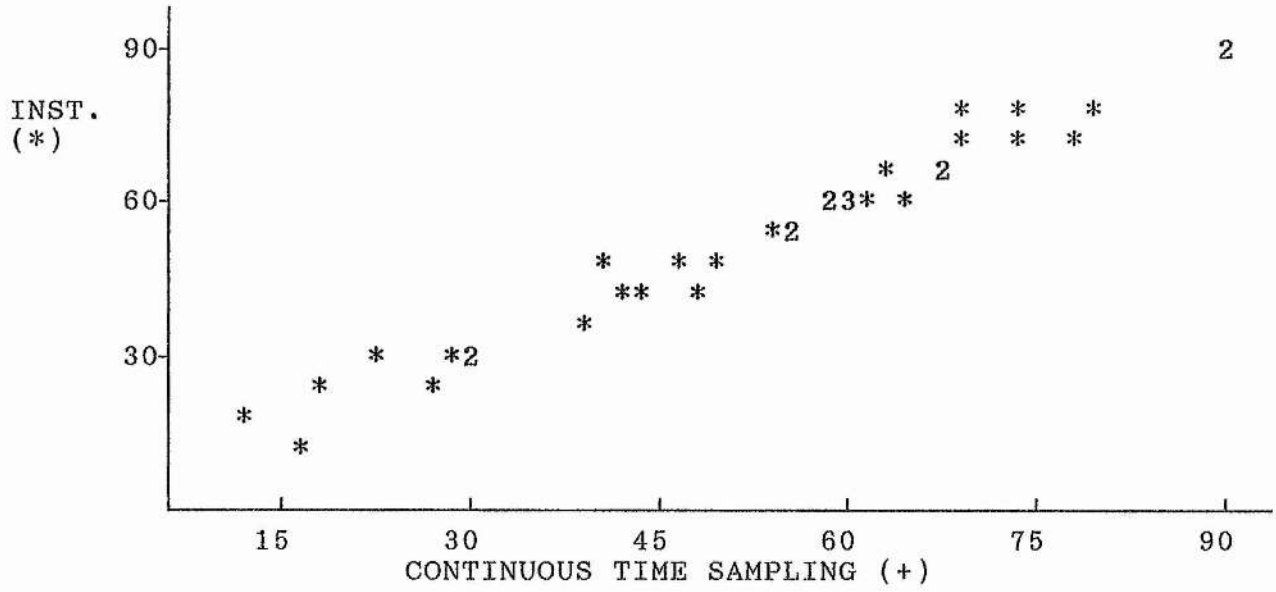
Laboratory based experiments on zebra finch song learning have sometimes involved housing birds in sound proof chambers, so that their auditory stimulation could be closely controlled; in many cases, however, birds have been kept in large rooms, where many individuals could be heard, in addition to the intended tutors. Learning from individuals that could not be seen at close quarters, or that could only be heard, has usually been argued not to occur.

One bird in the present experiment *did* seem to have copied at least one of its elements from a bird that was housed in a separate cage, and that it could not see. This possibility was discovered purely by chance, as the element involved had

a particularly unusual structure. Such a finding does not cast any doubt on previous results - the preference for learning from a tutor that can be seen and heard at close range is great. It is possible that elements previously unassigned to particular tutors might also have had such an origin, and were not all improvised.

Finally, an unexpected result from this experiment was that a significantly imbalanced sex ratio of offspring occurred depending on whether it was the father or the mother that was grey. In the former case, more females reached independence, while in the latter, more males reached independence. Records of early chick mortality were not kept. Further study would be needed to discover whether this effect was, for example, the result of differential parental investment.

Appendix 3.1 Comparison of perch preference results, obtained using instantaneous sampling and continuous time sampling



* - % of time samples (using instantaneous sampling) within close proximity of white model.

+ - % of time (minutes) spent within close proximity of white model.

Appendix 3.2 Testing for brood effects.

The following are the preferences exhibited by juveniles in the current study, with siblings grouped:

(F - father's morph preferred, M - mother's morph preferred)

Male song tutor preference.

FFF F F F F FF MMM FMM F

Male mate preference.

MM M M MF MF FFFF M

Female mate preference.

M MMM FMM F M M MMM M FMM FM

To investigate whether individuals act independently within broods, the "log likelihood ratio" test, or G-test, (see Sokal and Rohlf 1981) can be used.

With a brood i of size n_i, the number of individuals that prefer x can be represented by the binomial (n_i, θ_i).
The null hypothesis is that $\theta_i = \theta$.
ie. that the proportion preferring x in brood i, is no different from the overall proportion (θ) preferring x.

The probability of x_i in a particular brood is

$$\binom{n_i}{x_i} \cdot \theta_i^{x_i} \cdot (1 - \theta_i)^{n-x_i}$$

If all broods are different (implying that there is no information about i), then the the best estimate of θ_i is $\frac{x_i}{n_i}$.

The overall probability of x_i over all data is then

$$P_O = \binom{n_1}{x_1} \cdot \left(\frac{x_1}{n_1}\right)^{x_1} \cdot (1 - \frac{x_1}{n_1})^{n_1-x_1} \cdot \binom{n_2}{x_2} \cdot \left(\frac{x_2}{n_2}\right)^{x_2} \cdot (1 - \frac{x_2}{n_2})^{n_2-x_2} \cdot \text{etc}$$

If the pattern of preference is the same across all broods, then the best estimate of each θ_i is $\frac{\Sigma x_i}{\Sigma n_i} = a$.

The overall probability in this case is

$$P_A = \binom{n_1}{x_1} \cdot a^{x_1} \cdot (1 - a)^{n_1-x_1} \cdot \binom{n_2}{x_2} \cdot a^{x_2} \cdot (1 - a)^{n_1-x_2} \ldots \text{etc}$$

The Deviance (≡ chi-squared) is $2\log \frac{P_O}{P_A}$

(continued)

Using these formulae on the data from the experiment, we get:

Male song tutor preference. Deviance = 6.97, df = 8, $p > 0.5$

Male mate preference. Deviance = 5.39, df = 6, $p > 0.1$

Female mate preference. Deviance = 3.99, df = 9, $p > 0.9$.

The null hypothesis cannot be rejected in any of the three cases. Therefore, a brood effect could not be proven.

CHAPTER 4: INVESTIGATING CAUSAL REASONS FOR THE SELECTION OF THE FATHER AS THE SONG MODEL

4.1 Introduction

It has been shown in laboratory studies that a young male zebra finch will usually produce a song closely resembling that of his father, if the latter is present during the sensitive phase (see Chapter 1). This has applied to both normally-raised birds (Böhner 1983), and to female-raised ones (Eales 1987b).

Böhner (1983) housed two pairs in the same cage, but separated by a mesh partition. Both pairs had nest boxes, but only one pair was allowed to breed. At 40 days of age their offspring were put into a separate cage, positioned in front of the "neighbour" pair (but still within sight and sound of the parents). When the songs were recorded at 100 days, it was found that, of 11 males, nine had copied most or all of the song of the father, one had learnt all of its elements from the male neighbour and one had apparently improvised its song (with the exception of one element).

Eales (1987b) kept birds only with the mother up to 35 days, housed in a sound-proof chamber, and then introduced the father and an unrelated adult male into the cage. The birds remained in this situation for four to six months, at which stage their songs were recorded. All young males involved were found to have derived their songs wholly from the father.

What might have caused the father to be selected as song tutor in the above experiments? In neither case were detailed behavioural observations made, but Böhner suggests that the feeding of the young by the parents may have been important in his work. More recently, Williams (1990) argued that the amount of parental care, including feeding, influenced song tutor choice in the zebra finches she studied in an aviary. It is also possible that there was an influence of parental aggression prior to 40 days, during the stage in which the young are being forced into independence, or of the relatively higher exposure to the song of the father in the early post-hatching period, due to his greater proximity. More simply, the reason might lie with greater attention being paid to the father throughout the 100 days, because of the close bond formed with him during the period of dependence.

In Eales' experiment, the young had only very brief contact with the father prior to the tutoring period (the first four days of life). However, they may have learnt preferentially from him because of his relationship with the mother when they were reunited. Within hours of the introduction of the two males, Eales noted an "obvious separation" in the cage, with the mother and father re-establishing their bond, while the young generally remained in a group with the second male. In such circumstances the father could have been selected because of behaviour associated with pairing, such as directed song and soliciting by the female. The unpaired male did not appear to court the female beyond a short period immediately after having being put into the cage.

Alternatively, the father may have been more aggressive to the juveniles, and this might have had an impact (Eales noted that the fathers had a greater tendency to defend a particular area of the cage).

Less plausible possibilities would be that the young learnt to identify features of the father's song, or perhaps the distance call, from the period before he was removed, and were thus able to recognise him when he reappeared, at 35 days. It might even be possible that birds are genetically biassed to learning songs of one type rather than another (Marler 1970), but it would seem highly unlikely that this could allow differentiation between the song of the father and of another normally-singing zebra finch male, especially in view of the very strong influence of learning in the song acquisition process.

In this chapter, I describe further studies on the causes of song tutor choice in such situations. In particular, I examined whether it is the father's relationship with his offspring that is important, or whether learning from him is simply the result of increased exposure to his song, or of his greater aggression. It is possible that the paired status of the father *per se* was a major factor in the results of Eales, and so this was looked at, by using only unrelated birds. Also the effects on song learning of separating the parents was investigated.

Three experiments were carried out. The methods and results for each will be presented in turn, in the order in which they were performed.

4.2 Experiment 1 : Do zebra finches prefer to learn their songs from a paired tutor?

Broods were housed with their parents to 35 days. Other birds could be heard, but none were visible at a distance of less than three metres. Following the protocols of Eales and of Böhner, nest boxes were left in the breeding cages after the young had fledged (this is important, because removing them when the young are about 30 days old has been shown to affect the timing of song learning; see Slater and Richards, 1990).

From 35 to 100 days, each brood was transferred to the central section of a triple-cage, each part of which measured 75cm by 40cm by 40cm. The young were separated by mesh partitions from a single adult male on one side and from an established pair of birds on the other. Physical interactions were thus prohibited both between the juveniles and the tutors, and between the pair and the single male. Altogether 27 males from 14 broods were reared in this experiment. Twenty one different adult males were used as tutors.

The aim of this procedure was to establish whether or not birds (as may have been the case in Eales' experiment) might

select the father as their song model simply because of his paired status, rather than because of his, or the mother's, relationship to them.

Eales' housed all birds together in one cage in a sound-proof box. For consistency, a similar approach was initially adopted here. However, in two out of five cages organised in this way, levels of aggression were very high: in one case, the single tutor was badly pecked, and had to be removed, and in the other the paired male was attacked and killed by the single male. As a consequence, and also because it is not easy to make behavioural observations of birds in sound-proof boxes, the design was altered to that described above. [Of the three young males that *did* progress through the sound-proof box regime, two learnt their songs from the paired male, while the other learnt from the single male].

SONG ANALYSIS

Songs of the young males were recorded between days 100 and 120, using a Uher 4000 tape recorder, and were sonagrammed using a Kay Digital Sonagraph 7800. Sonagram analysis was done by eye. It was generally straightforward to determine which elements were derived from which tutor. When a decision could not be made, because either neither or both of the tutors seemed to possess the element in question, then the element was labelled as "unassigned". The song learning measure used in this experiment was the percentage of a young male's song derived from the songs of each of the potential tutors.

BEHAVIOURAL OBSERVATIONS

Ten 20-minute observations per cage were made on 10 of the 14 tutoring cages used in this experiment. They were carried out between 08.30 and 11.30, and spread throughout the period from 35 to 65 days. These watches involved 20 of the 27 young males and their tutors. The following data were recorded:

- "directed" (courtship) and "undirected" song of the tutors (total number of phrases).

- the frequency of copulations by the pair.

- the frequency of allopreening by the pair, scored by one-zero sampling every minute. The latter was considered more appropriate than instantaneous time-sampling because, although the behaviour occurs in bouts lasting a number of seconds (but usually less than a minute), active preening tends to stop and start; this sometimes makes it difficult to decide if preening is in progress at a precise moment.

[- obvious aggression by the adults, directed to the young birds. The intention was to record the number of threat calls (a distinctive, harsh vocalisation), and the frequency of flights at the partitions made by the adults. However, the former did not occur at all and it was not always possible to identify when aggressive intent was involved in the latter, so these data were discarded.]

- perching positions of the juveniles, measured by instantaneous sampling every 30 seconds to determine whether the young birds had a social preference for the pair or the single male. Juvenile males were scored as being either in

the third of the cage nearest the pair, in the third nearest the single male, or in the central region of the cage (where the food and water were positioned). Each cage contained two perches placed symmetrically, with one in the left third and one in the right.

Observations did not begin until 40 days or later because it was difficult separating males from females for a short period after their introduction to the tutoring cage at 35 days. As male siblings remained hard to distinguish individually throughout, counts were made simply of the number of young males at the left and right sides of the cage. The resulting preferred perching positions must therefore be treated with a degree of caution, bearing in mind that a high value for, say, the single male's side of the cage, *could* be a consequence of just one of a pair of brothers having a particularly strong preference for that location.

In addition to the above observations, further data were collected on the relative song output of the two tutors, for 11 of the 14 cages. This was done by recording a 45 minute tape of the birds' vocalisations, and counting up the phrases sung by each tutor during replay. It was always easy to separate the songs of the two tutors, but it was not possible in this case to determine whether phrases were "directed" or "undirected".

4.3 Results

The song learning patterns of the 27 young males involved in this experiment are shown in Table 4.1. Firstly, it can be seen that either the paired male or the single male were used as the main song model in all cases, with very few elements being copied from the father. This is in agreement with the results of a variety of other studies (for example, Eales 1985b, Clayton 1987b,c and Chapters 2 and 3 of this thesis), which have shown that zebra finches will usually learn the songs of tutors encountered after 35 days, if they are no longer exposed to the father.

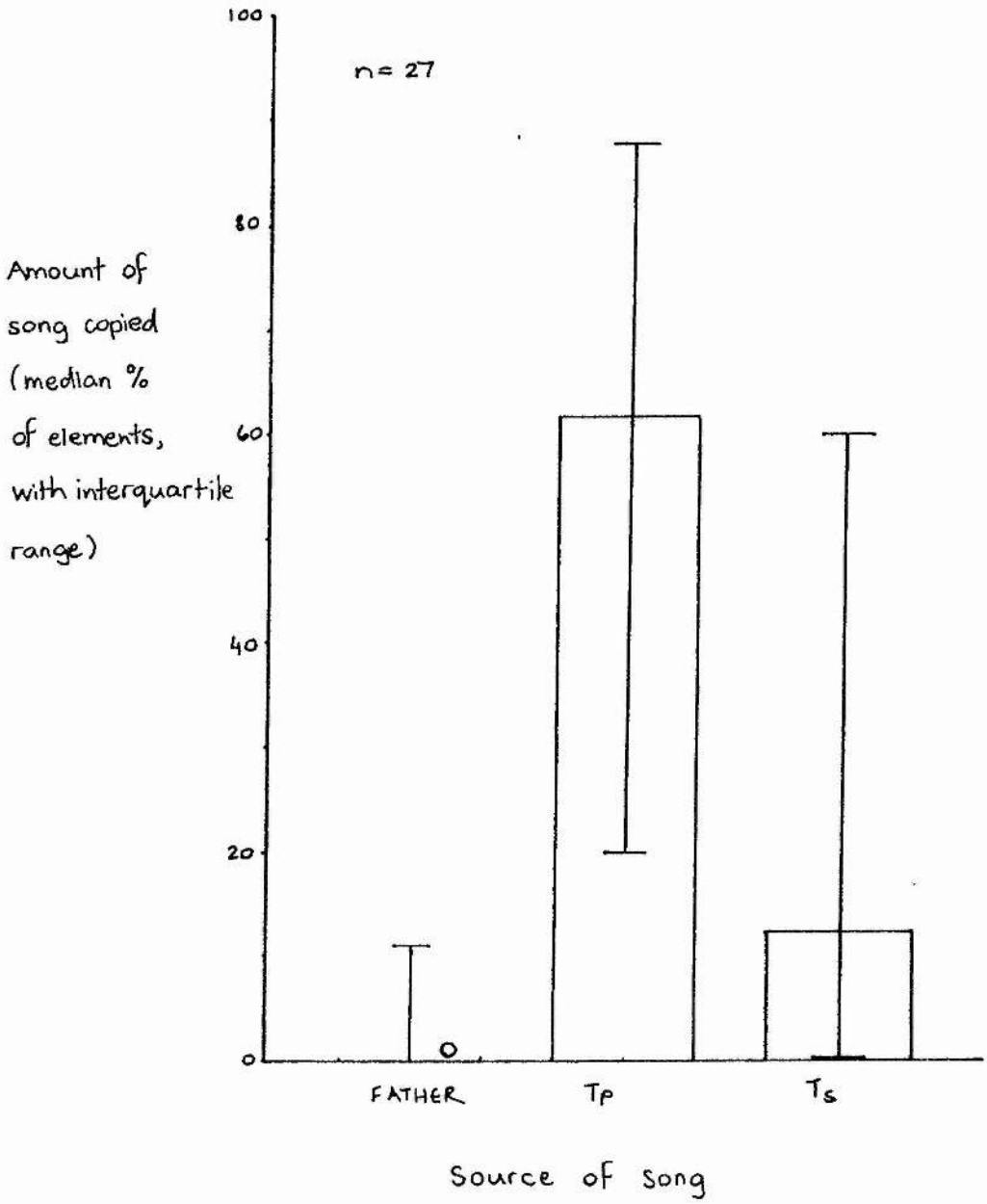
Figure 4.1 shows the median percentages of song copied from the three possible song models. There is a tendency to prefer the paired male as the song tutor, although this is insignificant when only the predominant preference of each bird is considered (Table 4.2). If we also take into account the strengths of the individual preferences, by considering the percentage of each bird's song copied from the two tutors, then the effect is significant (Wilcoxon matched pairs test; n for test = 25, W = 240, p = 0.038).

Siblings were housed together throughout the experiment. Can they be regarded as independent in terms of their tutor selection? To prove this is not easy. The fact that some brothers made quite different choices of song tutor in the present experiment (for example, see data for broods 1, 8 and 13, Table 4.1), does not imply that a sibling influence (or an influence due to shared tutors) did not exist in others. However, a reasonable indication of independence could be obtained if pairs of brothers could be shown to

Table 4.1 The amount of song learnt from the father, and from the paired and unpaired tutors, in experiment 1.

Brood	Young males	Source of song elements (as % of whole song in parentheses) FATHER	PAIRED TUTOR (Tp)	UNPAIRED TUTOR (Ts)	UNASSIGNED
1	DG72	0 (0)	8 (100)	0 (0)	0 (0)
1	DG73	2 (20)	0 (0)	7 (70)	1 (10)
1	DG74	0 (0)	6 (100)	0 (0)	0 (0)
2	R71	0 (0)	0 (0)	5 (71.4)	2 (28.6)
3	R201	0 (0)	7 (100)	0 (0)	0 (0)
4	R207	1 (12.5)	0 (0)	5 (62.5)	2 (25)
5	R172	1 (16.7)	4 (66.7)	0 (0)	1 (16.7)
6	R161	0 (0)	3 (50)	3 (50)	0 (0)
6	R164	0 (0)	5 (71.4)	1 (14.3)	1 (14.3)
7	O207	2 (15.4)	4 (30.8)	3 (23.1)	4 (30.8)
7	O208	1 (14.3)	5 (71.4)	0 (0)	1 (14.3)
7	O209	0 (0)	4 (80)	0 (0)	1 (20)
8	O244	0 (0)	8 (100)	0 (0)	0 (0)
8	O245	0 (0)	1 (20)	3 (60)	1 (20)
9	O228	0 (0)	0 (0)	8 (100)	0 (0)
9	O226	0 (0)	2 (40)	3 (60)	0 (0)
10	O222	1 (11.1)	0 (0)	4 (44.4)	4 (44.4)
10	O223	0 (0)	2 (33.3)	2 (33.3)	2 (33.3)
11	O224	0 (0)	7 (87.5)	0 (0)	1 (12.5)
11	O195	0 (0)	7 (100)	0 (0)	0 (0)
11	O197	0 (0)	3 (37.5)	1 (12.5)	4 (50)
12	O270	1 (7.7)	8 (61.5)	0 (0)	4 (30.8)
13	LG120	2 (20)	0 (0)	7 (70)	1 (10)
13	LG117	1 (9.1)	9 (81.8)	1 (9.1)	0 (0)
13	LG119	0 (0)	7 (87.5)	1 (12.5)	0 (0)
14	LG65	0 (0)	6 (66.7)	1 (11.1)	2 (22.2)
14	LG62	0 (0)	4 (50)	1 (12.5)	3 (37.5)

Figure 4.1 Song model preference in experiment 1, where young males were presented with a choice of learning from the father (before 35 days), or from a paired or single tutor.



Tp : Paired tutor

Ts : Single tutor

Table 4.2 Song tutor preferences in experiment 1

		Number of birds
Principal song tutor	Tp	17
	Ts	8

Tp - paired tutor
Ts - single tutor

Binomial test, n = 25, k = 8, p = 0.054.

(2 birds involved in the experiment copied the same number of elements from both tutors).

have differed from each other in their preferences, as much as did young males from different broods. Table 4.3 shows this to be indeed the case, with the data analysed in two different ways. This suggests that it is reasonable, with a degree of caution, to follow Eales and Böhner and treat siblings as independent.

Table 4.4 presents the behavioural data collected during the experiment. (Note - three broods were not observed, and sufficient data were only collected on tutor song output for brood 4).

The song rates, of the 22 tutors for which it was measured, varied from 12 to 376 phrases per hour. There was no difference in the overall rate of song between the paired and unpaired tutors (one-way analysis of variance, $F = 0.98$, $p = 0.333$).

The greatest difference in output occurred in the case of brood 7, with the single tutor singing 7.1 times more phrases. Despite this discrepancy, the three brothers in the brood all preferred the paired male as song tutor. In six cases all or most males within a brood showed a preference for learning from the tutor that sang the most, while in the other five cases the opposite was true.

Directed song from the adult males to the juveniles was relatively rare. It was recorded for five of the 11 single tutors, and for two of the 11 paired tutors. The highest rates were sung by the single tutors of broods 5 and 7, yet

Table 4.3i Percentage differences in the amount of song copied from the paired tutor in experiment 1, for brother pairs or for males from separate broods

	Differences between the % of song copied from the paired tutor for:	
	Brother pairs. (*)	Pairs of unrelated males, selected randomly.
1	100.0	28.8
2	0.0	40.4
3	21.4	71.4
4	49.2	33.3
5	8.6	50.0
6	80.0	50.0
7	40.0	67.5
8	33.3	37.5
9	12.5	80.0
10	62.5	26.0
11	81.8	16.7
12	87.5	30.8
13	16.7	100.0

Mann-Whitney U Test, one-tailed, $U = 168.0$, $p > 0.05$.

* - where there were three brothers within a brood, two randomly selected pairs were included.

Table 4.3ii Did sibling males agree in their overall song tutor preference more so than did pairs of non-siblings?

	Both preferred same tutor	Different tutor preferred
Sibling pairs	7	4
Non-sibling pairs	4	7

$X^2 = 1.636$, 1 degree of freedom.
Critical value, one-tailed = 2.706, therefore, not significant.

Non-sibling pairs selected randomly. Data only included where both birds in a "pair" showed a preference for one or other of the tutors.

Table 4.4 Behavioural data from experiment 1.

Male	Song output* Tp	Ts	Directed song output Tp-female	Tp-juvs	Ts-juvs	Allopr +	Cop$_a$	Perching pref$_b$ Tp	Ts
DG72 DG72 DG74	275	99	9	5	9	2	0	40	22
R201	44	141	0	0	0	0	0	41	20
R207	99	198	-	-	-	-	-	-	-
R172	220	147	18	0	21	12.9	0	41	30
R161 R164	53	12	0	0	0	0	0	58	24
O207 O208 O209	31	219	3	2	9	1.8	0	62	19
O244 O245	174	178	14	0	0	2.4	0	33	44
O228 O226	202	159	22	0	1	0.9	2	22	28
O222 O223	108	254	11	0	0	1.8	0	32	33
O224 O195 O197	86	376	9	0	2	0.3	0	39	33
O270	131	56	6	0	0	2.1	1	22	10

Tp - Paired tutor Ts - Single tutor
* - Song output measured in phrases/hour.
+ - Allopreening. Minutes in which observed per hour.
a - Copulations. Number of occurrences over all 10 watches.
b - Perching preference. % of time spent by male(s) at the side of the paired or the single male.

No data collected for R71, LG117, LG119, LG120, LG62, LG65. Only four watches made on R207, so only data on its tutors' overall song rates were entered. Data for other birds based mainly on ten 20-minute focal watches for each, although further time was spent collecting information on song output.

the paired male was the preferred tutor for both these broods, implying that this aspect of song could not have strongly affected song tutor choice.

It is possible that paired males are generally preferred as song models because some aspects of their behaviour are more likely to attract the attention of young males. Similarly, the preference for a particular paired tutor might be stronger in cases where such behaviours occur more often. Relevant intra-pair behaviours could include directed song from the male to the female, allopreening, copulations and sexual soliciting by the female.

The latter two seem to occur very rarely in established pairs denied the opportunity to breed. Only three matings were seen in 104 watches, covering nearly 36 hours in total. Two involved the pair with brood 9, while the other involved the brood 12 pair. Active female soliciting (crouching and tail-quivering) was only seen immediately prior to these matings.

Allopreening tended to occur at a similarly low rate for all pairs. In two cases it was not recorded at all, while for the rest the mean number of minutes per hour spent allopreening varied from 0.3 to 12.9. Directed song from the paired male to his mate varied from 0 to 22 phrases per hour, and thus occurred much less frequently than undirected song.

Neither of these latter measures correlated with the song preference for the paired tutor (Table 4.5). The correlation

Table 4.5 The relationship between the amount of song copied from the paired tutor, and the frequency of two behaviours associated with the formation and maintainance of pair bonds

Brood	Preference score for Tp as song tutor (1).	Rank	Allopr. freq. (2)	Rank	D.song to mate. (3)	Rank
1	44	6	2	4	9	5.5
3	100	1	0	9.5	0	9.5
5	67	3	12.9	1	18	2
6	29	8	0	9.5	0	9.5
7	53	5	1.8	5.5	3	8
8	30	7	2.4	2	14	3
9	-60	10	0.9	7	22	1
10	-22	9	1.8	5.5	11	4
11	71	2	0.3	8	9	5.5
12	62	4	2.1	3	6	7

1 - for each brood, the mean percentages of elements derived from the songs of the paired and single tutors were calculated. The value for the single tutor was then subtracted from that of the paired tutor.
2 - allopreening frequency, measured as the number of minutes in which it occurred per hour.
3 - frequency of directed song from the paired male to his mate, in phrases per hour.

Spearman rank correlations.

Song tutor preference for Tp versus allopreening frequency of Tp: $r = -0.012$

Song tutor preference for Tp versus frequency of directed song of Tp: $r = -0.390$

Allopreening frequency of Tp versus frequency of directed song to his mate: $r = 0.564$, $t = 1.93$, $p = 0.089$

between the amount of allopreening and the amount of directed song from the tutor to his mate approached significance (Spearman rank correlation, $r = 0.564$, $p = 0.089$). This is probably an indication that both broadly reflect the strength of a pair bond.

In seven of the 10 cages for which there are data, there was a preference for perching at the side of the cage nearest the paired tutor. In fact, the preference for being in this position was significant (Table 4.6i, Wilcoxon matched pairs test, $n = 10$, $w = 48$, $p = 0.041$). Furthermore, the young males that tended to stay closest to the pair learnt significantly more of their songs from the paired males than did the rest (Table 4.6ii, Mann-Whitney U Test, $U = 49$, $n = 7$, $m = 3$, $p < 0.05$), although an overall correlation between the percentage of time spent near to the pair and the amount of song copied from the paired male proved insignificant (Table 4.6iii).

4.4 Experiment 2 : Is song tutor choice guided more strongly by the presence of the father than by the presence of a paired male?

The previous experiment revealed a preference, bordering on significance, for learning from a paired male instead of from a single male. Such a preference could explain the results of Eales (1987b). However, there are other factors in her set-up, linked to the father's specific relationship with his offspring, that could have led to song learning

Table 4.6i The preferred perching positions of young males in experiment 1

Brood	Mean time spent near to the cage of the paired tutor (%).	Mean time spent near to the cage of the single tutor (%).
1	39.6	22.1
3	41.3	20.1
5	41.1	29.5
6	58.4	24.2
7	62	19.3
8	33.4	39.9
9	22.1	27.6
10	31.5	32.6
11	38.7	33.1
12	21.8	9.8

Wilcoxon matched pairs test, n = 10, w = 48, p = 0.041.

Table 4.6ii The relationship between preferred perching position of the young males and song tutor choice

Song preference for the paired tutor (*), per brood, for:

Birds spending most time near to Tp.	Birds spending most time near to Ts.
67	60
100	20
67	17
61	
61	
75	
62	

* - Mean percentage of song derived from the paired tutor, for each brood.

Mann-Whitney U Test, n = 6, m = 3, U = 49, $p < 0.05$.

Table 4.6iii Correlation in experiment 1, between the amount of time spent in close proximity to the paired tutor by young males, and the amount of song copied from him

Brood	Mean time spent near to the cage of the paired tutor (%).	Proportion of song derived from paired tutor (mean % of elements/brood)
1	39.6	66.7
3	41.3	100.0
5	41.1	66.7
6	58.4	60.7
7	62.0	60.7
8	33.4	60.0
9	22.1	20.0
10	31.5	16.7
11	38.7	75.0
12	21.8	61.5

Pearson correlation (after arcsine transformation): $r = 0.38$
Anova, about regression line: $F = 0.97$, $p = 0.35$, NS.

only from the father, in addition to the fact that he was paired.

The present and subsequent experiments were designed to investigate the importance of these other factors in the guiding of song tutor choice

Here, broods were housed with their parents to 35 days before being transferred together to triple cages. They were then given a choice of learning song from:
i) the father, housed alone in the cage on one side of the brood (separated by wire mesh),
or
ii) an unrelated, unfamiliar male, housed on the other side, in the same cage as the mother.

Strong predictions regarding the outcome of this experiment were not easy to make. Certainly a conflict could be envisaged between the preference for learning the song of the father (to whom the young had been exposed from hatching), and the preference for learning from the paired tutor (following the results of the first experiment). As the latter result was marginal, the song of the father was expected to be selected.

General methodological details were as those described for experiment 1, with behavioural data also collected in the same way. Altogether 13 males were reared from seven broods.

4.5 Results

The song learning results of the 13 males are shown in Table 4.7, and the median preferences are illustrated in Figure 4.2. The tutor housed with the mother was preferred, perhaps surprisingly, over the father as a song model; 10 birds learnt mainly from this unrelated tutor, two learnt mainly from the father and one learnt equally from both (using just direction of preference [Table 4.8] : binomial test, n = 12, k = 1, p = 0.038; using percentage values for each bird: Wilcoxon matched pairs test, n for test = 12, W = 9.0, p = 0.02).

In the first experiment, 63% of the tutees preferred the paired male as song tutor, while in experiment 2, he was preferred by 77% of the birds. However, this difference is not significant (see Table 4.9 and Figure 4.3).

Behavioural observations were made on six of the seven broods (see Table 4.10). As with experiment 1, there was no difference in the overall song rates of the "paired" and "unpaired" tutors (Wilcoxon matched pairs test, n for test = 6, W = 16, p = 0.30). Also, it was again highly unlikely that his song output was linked to the amount of song copied from a tutor, but there are too few data to test this statistically. The father (single tutor) for brood 7 sang at a very low rate, only six phrases per hour, nearly 35 times less than the paired tutor. Whether such a relatively low song output affected the tutor selection is impossible to judge - certainly three out of the four siblings involved here learnt mainly from the paired tutor,

Table 4.7 The amount of song learnt from the father and from the unrelated, paired tutor, in experiment 2.

Brood	Young males	Source of song elements (as % of whole song in parentheses) FATHER	PAIRED TUTOR	UNASSIGNED
1	O62	0 (0)	10 (100)	0 (0)
2	O200	1 (11.1)	6 (66.7)	2 (22.2)
3	O247	0 (0)	9 (90)	1 (10)
3	O249	1 (8.3)	8 (66.7)	3 (25)
4	O241	0 (0)	5 (83.3)	1 (16.7)
5	O211	1 (9.1)	5 (45.5)	5 (45.5)
6	O268	5 (71.4)	2 (28.6)	0 (0)
6	O269	5 (83.3)	1 (16.7)	0 (0)
6	O266	0 (0)	5 (71.4)	1 (14.3)
7	O159	2 (28.6)	2 (28.6)	3 (42.9)
7	O161	2 (25)	5 (62.5)	1 (12.5)
7	O162	0 (0)	8 (88.8)	1 (11.1)
7	O163	0 (0)	7 (70)	3 (30)

Table 4.8 Song tutor preferences in experiment 2

Using only directions of preference:

		Number of birds
Principal song tutor	Tp	10
	Ts	2

Tp - paired tutor
Ts - single tutor

Binomial test, n = 12, k = 2, p = 0.038.

Figure 4.2 Song model preference in experiment 2, where young males were presented with a choice of learning from the father, or from an unrelated male housed with the mother.

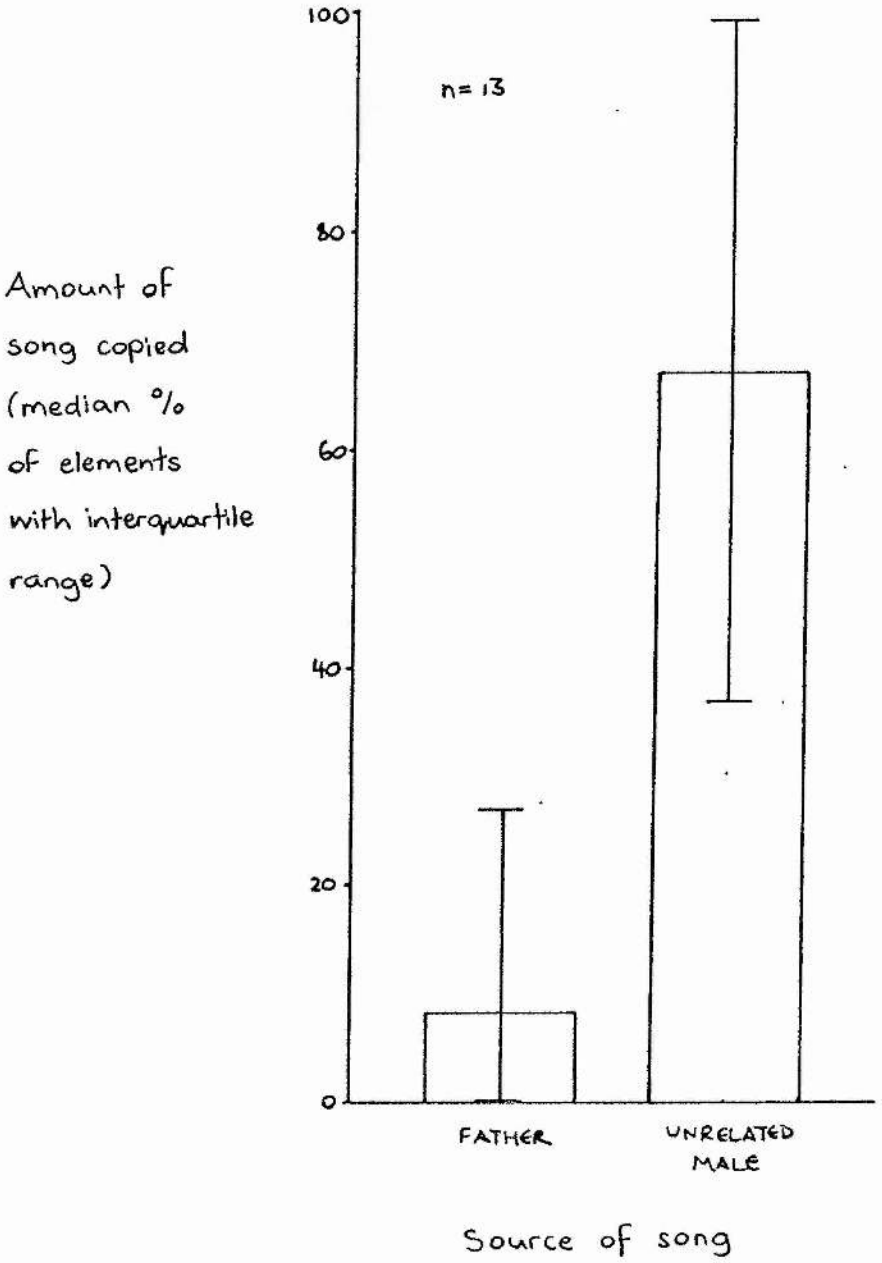


Table 4.9 Comparison of the strength of preference for the paired male as song tutor, between experiments 1 and 2.

i) By looking at preferred tutors :

	Preferred tutor	
	Paired male	Single male
Experiment 1	17	8
Experiment 2	10	2

Fisher exact test : p = 0.28
Not significant.

ii) By considering percentages of elements copied from paired tutor for each bird.

Preference for paired male (*):

Experiment 1	Experiment 2
100.0	100.0
0.0	85.7
100.0	100.0
0.0	88.9
100.0	100.0
0.0	83.3
100.0	100.0
50.0	28.6
83.3	16.7
57.1	50.0
100.0	90.0
100.0	71.4
100.0	100.0
25.0	
0.0	
40.0	
0.0	
50.0	
100.0	
100.0	
75.0	
100.0	
0.0	
90.0	
87.5	
85.7	
80.0	

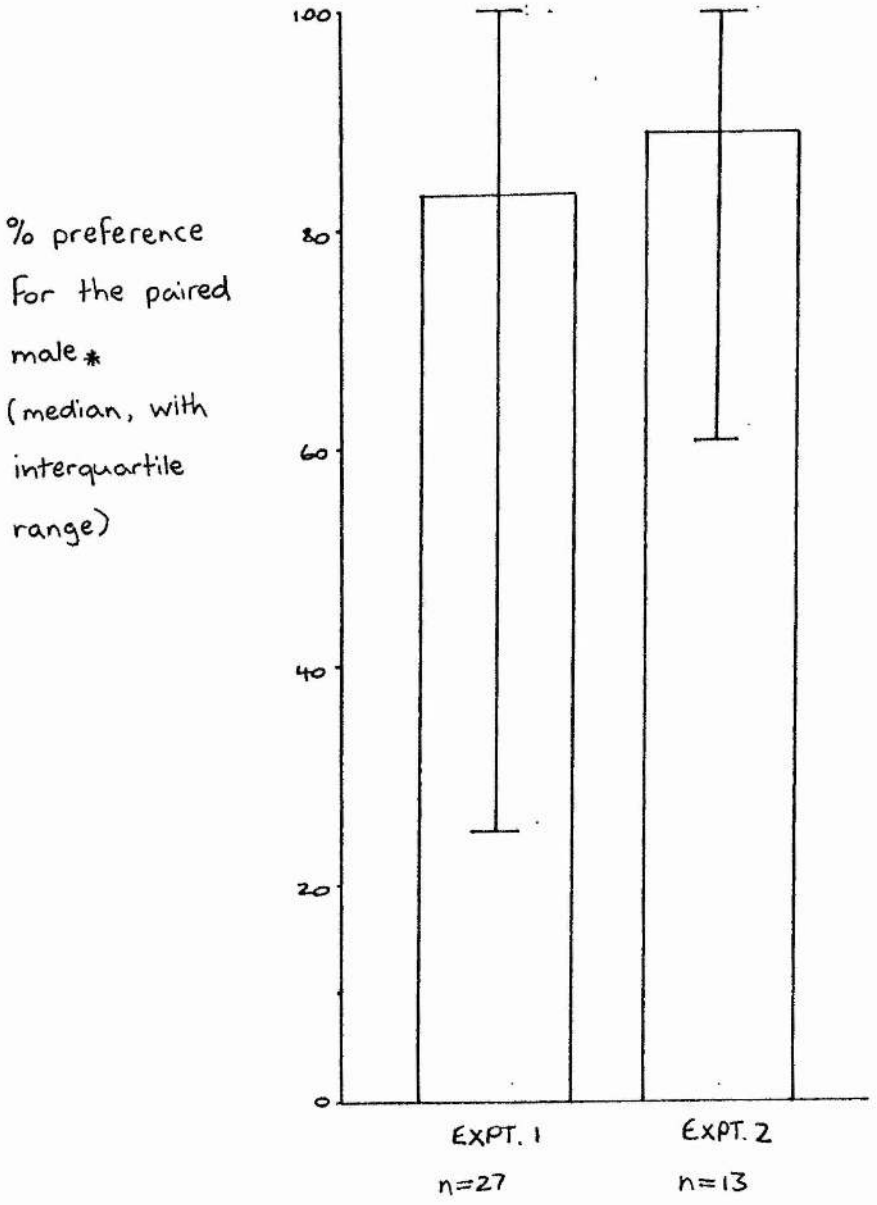
Mann-Whitney
U Test:

n = 27, m = 13, U = 520,
p = 0.32

$$* = \frac{\text{Elements copied from Tp}}{\text{Elements copied from Tp or Ts}} \times 100$$

(this excludes any effect of unassigned elements)

Figure 4.3 Comparison of the strength of preference for learning from the paired tutor, in experiments 1 and 2.



$$* = \frac{\text{Elements copied from paired male}}{\text{Elements copied from paired or single male}} \times 100$$

Table 4.10 Behavioural data from experiment 2.

Male	Song output* Tp	Ts	Directed song output Tp-female	Tp-juvs	Ts-juvs	Allopr +	Cop[a]	Perching pref[b] Tp	Ts
O200	222	97	10.5	0	0	0.6	1	39	25
O247 O249	193	159	2.4	0	0	1.8	1	41	29
O241	164	49	22.2	0	0	1.2	0	33	30
O211	24	131	6.6	2.7	6	0.9	0	37	14
O268 O269 O266	71	151	6.3	1.5	0	0	0	41	22
O159 O161 O162 O163	208	6	12.6	0	6	0	0	52	13

Tp - Paired tutor Ts - Single tutor
* - Song output measured in phrases/hour.
+ - Allopreening. Minutes in which observed per hour.
a - Copulations. Number of occurrences over all 10 watches.
b - Perching preference. % of time spent by male(s) at the side of the paired or the single male.

No data collected for O62. Data for other birds based mainly on ten 20-minute focal watches for each, although further time was spent collecting information on song output.

but then so did most of the others. Also, there was at least some evidence of learning from the father (but this could have occurred before 35 days of age, when the father's song rate might have been higher).

As with experiment 1, directed song to the juveniles was rare (1.5 to 6 phrases per hour) for the four birds, two paired and two unpaired, that showed it.

Directed song from the "paired" male to the adult female occurred at a rate that varied from 2.4 to 22.2 phrases per hour. There was no correlation between this and the amount of song copied (Table 4.11). Directed song to the female was no more prevalent in experiment 1, where the "pair" was well established, than in experiment 2, where the male and female were put together at the start of the experiment (Mann-Whitney U Test, $U = 54$, $p = 0.79$).

Similarly, there was no evidence of there being more copulations in the first experiment. There was an indication of a slight tendency for more allopreening in experiment 1, but this was not significant (Table 4.12). The lack of a difference in these various measures is, in one way, useful: if established and newly set up pairs are not grossly dissimilar in terms of their intra-pair behaviours, then the results are more likely to be due to the constitution of a pair in terms of bird familiarity and kinship. Otherwise, we would have a further variable to consider, related to the bond strength of the male and female.

Table 4.11 The correlation between the directed song output of the paired male and the amount of song copied from him, in experiment 2

Brood	Directed song to female (phrases/hour)	Percentage of song copied from paired male (mean/brood)
2	10.5	66.7
3	2.4	78.4
4	22.2	83.3
5	6.6	45.5
6	6.3	24.6
7	12.6	77.9

Spearman rank correlation: $r = 0.429$, $df = 4$, $p > 0.05$.

Table 4.12 Frequency of allopreening in experiments 1 and 2

	Allopreening frequency (minutes/hour in which recorded)		
	0 - 1	1 - 2	2+
Experiment 1	4	3	3
Experiment 2	4	2	0

Fisher exact test (combining data from last two columns) : $p = 0.30$
Not significant.

Table 4.13 The preferred perching positions of young males in experiment 2

Brood	Mean time spent near to the cage of the paired tutor (%).	Mean time spent near to the cage of the single tutor (%).
2	39.0	24.5
3	40.6	29.0
4	32.8	30.0
5	36.9	14.4
6	41.3	21.8
7	51.5	13.0

Wilcoxon matched pairs test, $n = 6$, $w = 21$, $p = 0.036$.

The pattern of preferred perching locations followed that of experiment 1, with birds showing a significant tendency to sit nearest the pair (Table 4.13). There was no correlation between the percentage of song elements derived from the paired tutor and the proportion of time spent near to his cage (Table 4.14).

As there was a slight indication of juveniles more strongly preferring the paired male as song tutor in this experiment, than did those in experiment 1, it was possible that these young males were also tending to spend more of their time in close proximity to this bird. This, however, was not the case (Table 4.15).

Table 4.14 Correlation in experiment 2, between the amount of time spent in close proximity to the paired tutor by young males, and the amount of song copied from him

Brood	Mean time spent near to the cage of the paired tutor (%).	Proportion of song derived from paired tutor (mean % of elements/brood)
2	39.0	66.7
3	40.6	78.4
4	32.8	83.3
5	36.9	45.5
6	41.3	24.6
7	51.5	77.9

Spearman rank correlation: $r = -0.2$, $df = 4$, $p > 0.05$.

Table 4.15 Do young males spend more time near to the paired tutor in experiment 2 than in experiment 1

Percentage of time spent close to paired tutor:

Experiment 1 males	Experiment 2 males
39.6	39.0
41.3	40.6
41.1	32.8
58.4	36.9
62.0	41.3
33.4	51.5
22.1	
31.5	
38.7	
21.8	

Mann-Whitney U Test, $n = 10$, $m = 6$, $U = 81.5$, $p = 0.74$, NS.

4.6 Experiment 3 : The effect on song tutor choice of housing the mother and father apart, each with a new partner.

The father was largely avoided with regard to song learning in experiment 2, with birds preferring an unfamiliar male caged with the mother. This preference may have been because of the paired status of the unrelated male. If so, then using a similar regime, but providing the father with a new mate should cause a strong switch in song tutor choice, such that he now becomes the preferred tutor (as per Böhner 1983). However, the mother may also have been a factor - perhaps greater attention to her influenced tutor choice. In this case, the switch towards a preference for the father's song would not occur, or would be less complete.

As with experiments 1 and 2, broods were housed with both parents for the first 35 days of life, before being transferred to triple cages. They then had a choice of learning their songs from:

i) the father, housed with an unfamiliar, unrelated female, or

ii) an unfamiliar, unrelated male, housed with the mother.

General methodological details were as described for the previous experiments, although no data were collected on tutor behaviour. 16 young males from 9 broods went through this experiment.

4.7 Results

10 males learnt more of their songs from the father, while six preferred the unrelated tutor (Table 4.16). This difference is not significant (Figure 4.4 and Table 4.17: binomial test, $n = 16$, $k = 6$, $p = 0.227$; also, Wilcoxon matched pairs test, $n = 16$, $W = 98$, $p = 0.127$). The only difference between the regime of this experiment, and of the last, was that then the father was not provided with a partner in his cage. This resulted in the reduced popularity of him as a song tutor (Table 4.18 and Figure 4.5).

4.8 Discussion

The inspiration for this study came from the results of Eales (1987b) and Böhner (1983). They showed that young male zebra finches will learn the song of their father, in preference to that of an unrelated male, if they are exposed to both during the sensitive phase for song development. Eales found this even though her birds were raised to independence by only the mother.

An important issue in this experiment, and other similarly designed ones, concerns sibling males and whether or not their song tutor selections can be regarded as being independent. In the present context, non-independence will ensue if:

Table 4.16 The amount of song learnt from the father and from the unrelated tutor, in experiment 3.

Brood	Young males	Source of song elements (as % of whole song in parentheses) FATHER	UNRELATED TUTOR	UNASSIGNED
1	LG175	6 (75)	1 (12.5)	1 (12.5)
1	LG176	3 (75)	0 (0)	1 (25)
2	LG115	8 (100)	0 (0)	0 (0)
2	LG113	1 (25)	3 (75)	0 (0)
2	LG114	9 (100)	0 (0)	0 (0)
3	O644	9 (90)	0 (0)	1 (10)
3	O645	10 (100)	0 (0)	0 (0)
3	O647	8 (100)	0 (0)	0 (0)
4	O641	0 (0)	7 (87.5)	1 (12.5)
4	O642	0 (0)	8 (100)	0 (0)
5	LG233	0 (0)	10 (100)	0 (0)
6	LG172	8 (88.9)	0 (0)	1 (11.1)
7	O620	0 (0)	6 (66.7)	3 (33.3)
8	O994	7 (100)	0 (0)	0 (0)
8	O993	5 (100)	0 (0)	0 (0)
9	LG110	5 (35.7)	7 (50)	2 (14.3)

Table 4.17 Song tutor preferences in experiment 3

Using only directions of preference:

		Number of broods
Principal song tutor	F	10
	T	6

F - father

T - unrelated tutor

Binomial test, n = 16, k = 6, p = 0.227.

Figure 4.4 Song model preference in experiment 3, where young males were presented with a choice of learning from the father, housed with an unrelated female, or from an unrelated male, housed with the mother.

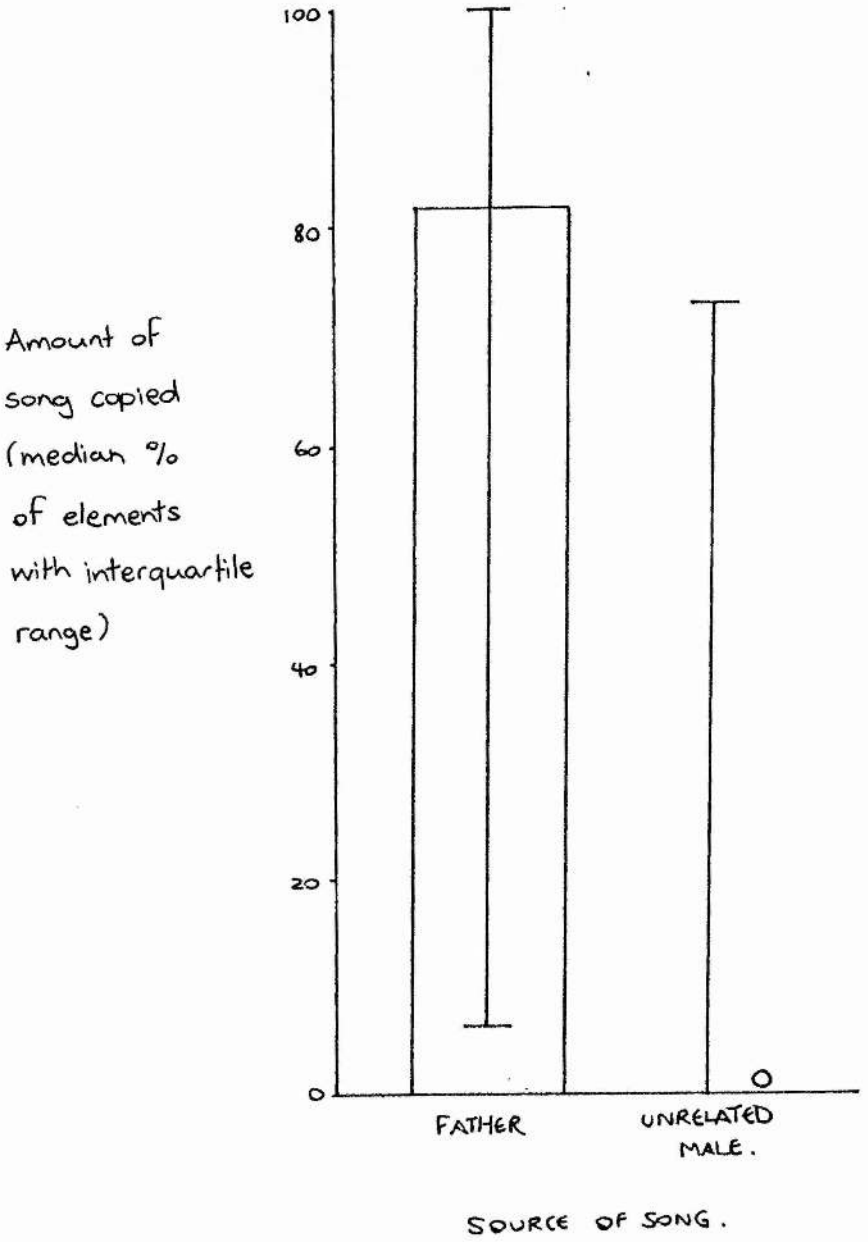


Table 4.18 Comparison of the strength of preference for the father as song tutor, between experiments 2 and 3.

i) By looking at preferred tutors:

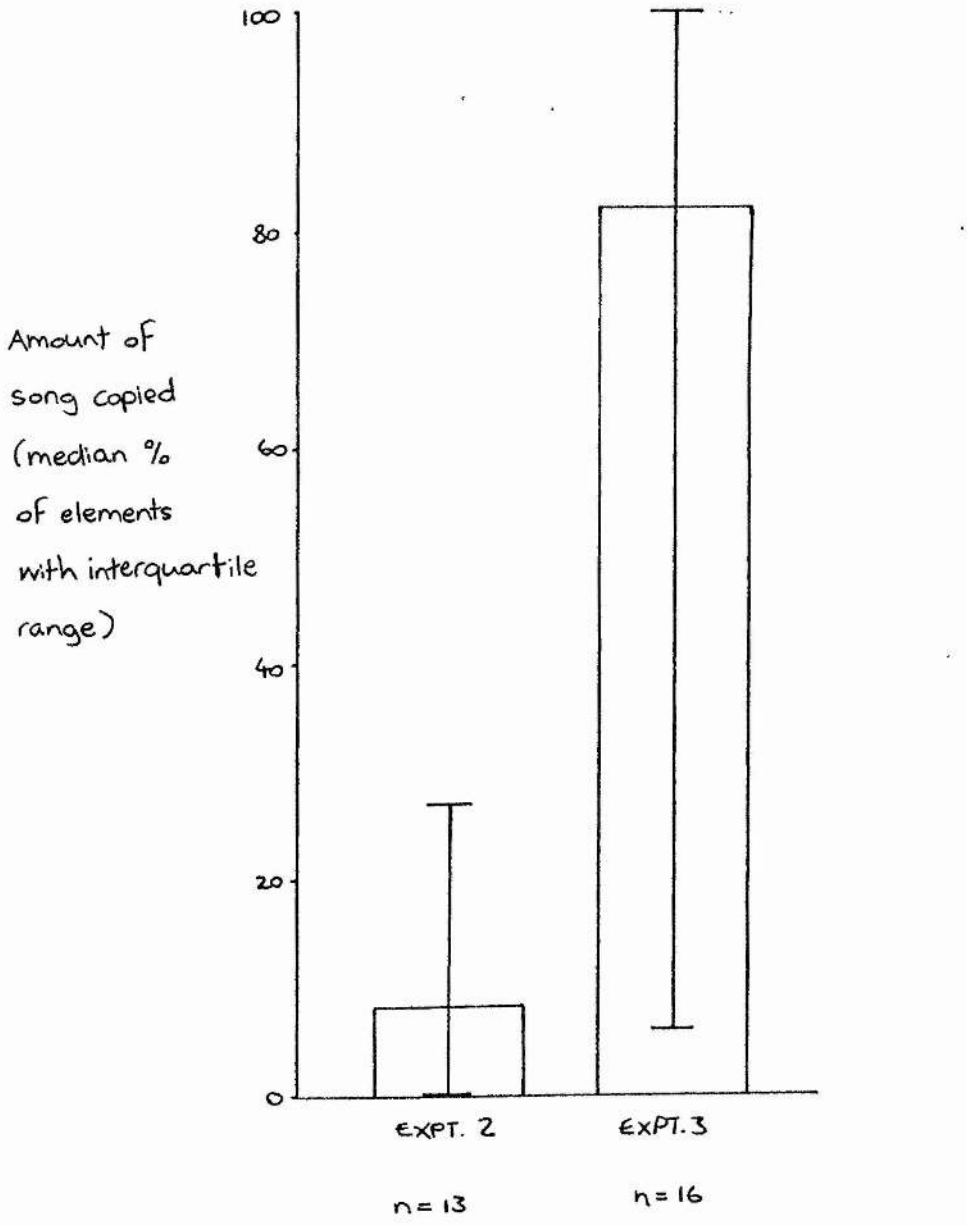
	Preferred tutor	
	Father	Unrelated tutor
Experiment 2	2	10
Experiment 3	10	6

X^2 = 5.88, 1 degree of freedom,
critical value = 3.84; significant.

ii) By looking at percentages of elements copied from father for each bird:

Experiment 2	Experiment 3	
0	75	
11.1	75	
0	100	
8.3	25	
0	100	Mann-Whitney
9.1	90	U Test:
71.4	100	
83.3	100	n = 16, m = 13, U = 140.5,
28.6	0	p = 0.016
10	0	
25	0	
0	88.9	
0	0	
	100	
	100	
	35.7	

Figure 4.5 Comparison of the strength of preference for learning from the father, in experiments 2 and 3.



i) brothers influence each other's song tutor selection in some way.

or

ii) differences in tutor song or behaviour, unrelated to those associated with paired status, affect tutor choice of young within a brood in an equivalent manner. For example, a tutor might have a particular song, or perhaps plumage characteristics, that render him more or less attractive as a song model.

Data presented in Table 4.3 did not reveal any pattern indicative of a sibling influence on song learning in the first experiment. Furthermore, brood effects could not be found in any of the three experiments using G-tests, as described in Appendix 3.2 (Chapter 3). The respective chi-square values, degrees of freedom and the probabilities (of independence) are as follows:
Experiment 1: $X^2 = 6.121$, $df = 13$, $p > 0.9$; Experiment 2: $X^2 = 3.08$, $df = 6$, $p > 0.5$; Experiment 3: $X^2 = 8.24$, $df = 8$, $p > 0.1$.

It is worth commenting, however, that to demonstrate non-independence would require a large sample of broods, particularly because there were usually only one or two males in each. It is possible that the sample sizes in this study were inadequate for investigating sibling effects.

Eales and Böhner, in their experiments, regarded siblings as independent in their song tutor choice. Eales argued that "most [siblings] did not develop songs like their brood

mates" and that, with birds reared in isolation from adult song, "the great variation between brothers .... shows that learning from siblings was not an important influence on them".

In Böhner's case, of 11 males, nine copied most or all of their songs from the father, while just one learnt the song of the unrelated "neighbour". Although this is a convincing result, the "nine" included two pairs of brothers and, without evidence to the contrary, these could be argued to be non-independent for either of the two reasons stated above. Furthermore, the nine broods that took part in the study were tutored by only seven unique father-neighbour combinations. It is not indicated which of the young males were exposed to the same tutors, but it is possible that those involved also all selected the father as song tutor. If so, they may have acted non-independently for reason ii).

This problem is not discussed by Böhner, who emphasises instead the differences that existed between the songs of brothers, and attributes them to "inaccurate copying". In fact, one pair of brothers learnt 100% and 67% of their songs from the father, while the figures for the second pair were 83% and 90%, suggesting quite a high level of agreement.

If the data that may not have been independent are excluded from Böhner's experiment, we are left with five birds showing a preference for the father's song, and one preferring the neighbour. The effect is then non-significant

(binomial distribution, n = 6, k = 1, p = 0.109), though perhaps because the data are so reduced.

How reliable, then, are their results? Despite the fact that some of Böhner's data may not have been independent, and that the sample size in Eales' experiment was only four, their findings are likely to be genuine, based on the results of other work: studies by Immelmann (1969) and Eales (1985b), as well as those described in Chapter 2, have all demonstrated a level of preference for learning song from the father, when he was available as a tutor throughout development. Accepting this, the aim here was to identify some of the causal reasons behind the selection of the father as the preferred song tutor.

The results of experiment 1 suggest that there is probably a preference for learning from a paired, rather than a single, tutor, though the effect only bordered on being significant. However, this may not be a weaker tutor selection than occurred in Eales' study, as her sample was so small. Furthermore, because of her experimental set-up, a stronger preference for the paired male could still have been explained without the need to consider the mother or father's relatedness to the tutees. Her tutors and tutees were all housed together, so there was the potential for more intense and varied interactions amongst them, which could have served to emphasise the difference in paired status. For example, paired males may well exhibit more aggression than single males, but any effect of this would

be nullified under the regime used here, because of the presence of wire mesh partitions.

Given the strong influence the father is known to have on song learning, a surprising result was obtained in experiment 2, where the unrelated male was preferred to the father as song tutor. The focus of attention of the young males may have been diverted away from the father for one or more of the following reasons:
i) that the unrelated male was housed with a female, whereas the father was not;
ii) that there was still a strong filial attraction to the mother, more so than to the father. If so, then the exposure to the unrelated tutor (and hence the likelihood of copying from him) would have been increased by indirect means, through his close proximity to the mother.

In experiment 3, the mother and father were again housed apart, but this time both were given a new partner. Providing the father with a mate produced a different result to that obtained in the previous experiment: this time more birds learnt from the father than from the unrelated male. He was clearly more favoured than in experiment 2. However, the father was still not *significantly* preferred to the unrelated male, in contrast to the results of Böhner's experiment, where the father was selected in nine out of 11 cases. This implies a strong influence of the mother on the guidance of tutor choice.

A summary of the results obtained here and by Böhner (1983) is shown in Table 4.19. Can it be concluded that there is genuinely a preference for learning from a paired male, rather than a single male, irrespective of the relatedness of the tutors to the offspring? The following alternatives are possible:

1. There is no preference *per se* for a paired male. The greater number of birds that copied from the paired male in experiment 1 may have resulted by chance. If so, the selection of the father as song tutor in Eales' study, and of the unrelated male in experiment 2 of the present study, must then have been the consequence of the mother's influence (which must, in the latter case, have been stronger than that of the father). However, these conclusions would make the results of experiment 3 hard to interpret: here most song should again have been copied from the male housed with the mother but instead, if anyone, the father was preferred.

2. There is a preference for a paired male. That is, the greater number of males that copied from the paired male in experiment 1 represented a real effect. If this is so, then the results of experiment 2 are explainable simply by the same type of preference.

Also, we must assume that the two parents exert a roughly equivalent influence on a young male's tutor selection: the mother indirectly, through attraction to her increasing exposure to her accompanying male; the father directly, by

Table 4.19 Summary of results.

Tutor choice 1	Tutor choice 2	Preference for:
FATHER Housed with: mother	UNRELATED MALE Housed with: unrelated female	FATHER (significant) Böhner 1983
UNRELATED MALE Housed with: unrelated female	UNRELATED MALE Housed alone	PAIRED MALE (significant?) Experiment 1
UNRELATED MALE Housed with: mother	FATHER Housed alone	PAIRED MALE (significant) Experiment 2
FATHER Housed with: unrelated female	UNRELATED MALE Housed with: mother	(FATHER) (not significant) Experiment 3

filial attraction, but perhaps also because of a preference developed for features of his song (Clayton, 1987b), or morphology. If the father's influence is substantially greater, then there should have been a stronger preference for him as tutor in experiment 2 than for the single male in experiment 1, but the opposite, if anything, was true. Had the mother's influence been the greater, then the unrelated male should have been the preferred song tutor in experiment 3, but again the bias was slightly in the reverse direction.

With the second of these alternatives, the preference for learning from the father in the studies by Eales and Böhner could be accounted for by, in the first case, a combination of filial attraction *and* the preference for a paired tutor, and by just the former of these in the second case.

Why should it be that juvenile zebra finches prefer to learn from a tutor with a mate? It might be a good strategy to learn from a male with a partner rather than from a single male, perhaps because the paired male's status could provide some indication about the attractiveness of his song to the opposite sex. This argument would hold more weight if there was evidence for female zebra finches having sexual preferences for particular song characteristics. Such evidence is lacking at present, although females certainly can discriminate between even quite similar songs, and have been shown to prefer to perch hearer to a speaker playing the song of the father, than to one playing that of a stranger (Miller 1979a,b).

If such an explanation is correct, then young males would need to have some means of discriminating between paired and unpaired adults. Various cues would be available for pair bond assessment, including copulation rate, nest sharing, directed song output to the female, sexual solicitation by the female and the long term presence of social behaviours such as allopreening and "clumping". In experiments 1 and 2, allopreening, copulations and directed song were measured, but there was no indication that the pairs in which they occurred more often were the most strongly preferred. Also, they did not occur at a higher frequency in experiment 1 than in experiment 2, despite the fact that the pairs in the first case were well-established, while those in the second had been artificially brought together. It could be that these criteria are not good predictors of pair bond strength. It is more likely though that they were not adequately measured. It is also possibile that differences are better perceived by zebra finches, or that pair bond strength is being assessed by some of the other factors listed above.

A preference for learning from a paired tutor can be accounted for without the need for a strictly functional explanation. There was a significant tendency in experiments 1 and 2 for young birds to prefer to spend most of their time nearest to the paired male. Also, in experiment 1, the proximity to the paired tutor was less for those birds that learnt most of their songs from him, than for birds that learnt mainly from the single tutor. Whether this difference

in proximity is a cause or consequence of song learning is not easy to assess.

If the former, it could be that juveniles simply prefer to join a larger group, for social and/or other reasons (such as part of an anti-predator flocking response). Once in close proximity, then the higher level of exposure to the song, and other behaviours, of the paired male would lead to the choice of him as song tutor.

Alternatively, the young males might first have developed a preference for the paired tutor for reasons related to his behaviour, and perched near to him as a consequence, resulting in a greater likelihood of song copying. For example, the paired male may have been involved in more stimulating (and numerous) interactions, because of the female's presence, resulting directly in more attention from the tutees. Such behaviours could have included those listed above; in addition, it was also possible that the paired tutor had a higher overall song rate (directed and undirected), or higher general activity or aggression levels. The first of these possibilities can be dismissed, as no hint of such an effect emerged from the behavioural analysis. The latter two were not investigated, but also seem unlikely to have had a large influence - tutor activity level did not increase learning performance in the experiment investigating the effect of distance on song learning (Chapter 6), and aggression could not have played a large part due to the presence of mesh partitions.

To summarise the principal findings of the present study, three general influences have been found that can affect song tutor choice in zebra finches. These are:
i) the presence of the father - there is a preference for learning from him.
ii) the presence of the mother - there is a preference for learning from the male she is partnered with.
iii) the presence of a larger group - there is a preference for learning from a paired male over a single male. (It has not been shown whether it was being accompanied by a female, or being simply part of a larger group, that caused this effect).

It is more difficult to assess which of the above exerts the greatest influence, although it is apparent that i) and ii) are similar, because no significant preference was shown for learning from either the father, or from the male housed with the mother, in experiment 3.

One way to approach the question would be to borrow an idea from game theory; that is, by allocating scores representing the importance of the various criteria as song learning stimuli, in such a way that the known results can be accounted for. These scores can then be used to make predictions about song learning patterns for, as yet, untried tutor combinations. Table 4.20 is a matrix containing the possible tutoring regimes that could be used to tease apart the various factors involved.

Table 4.20 Matrix of tutor combinations, suitable for teasing out the relative preference for paired or related males as song models

		Tutor 1					
		F + m	F + uf	F	U + m	U + uf	U
Tutor 2	F + m	X	X	X	X	1*	5
	F + uf	X	X	X	4*	6	7
	F	X	X	X	3*	8	9
	U + m	X			X	10	11
	U + uf					12*	2*
	U						13*

X - impossible combinations.

F - father
m - mother
U - unrelated male
uf - unrelated female

* - already carried out: 1. Böhner 1983
2. Experiment 1
3. Experiment 2
4. Experiment 3

Combinations 12 and 13, involving only unrelated birds, have been used widely in studies investigating behavioural and morphological influences on song learning.

In Table 4.21, three scoring systems are shown that adequately fit the known results. In the first, the influence of each parent is judged greater than that of paired status, while the opposite is true for system 2; both influences are equivalent in system 3. The predicted results for the missing data from the Table 4.20 matrix are shown, with the strongest preferences indicated by the largest differences in score.

The accuracy of such a scoring system depends on the reliability of the conclusions from experiments 1 to 3, and from Böhner's work. There is some room for doubt, because of the reservations covered earlier, about potentially non-independent data altering the strengths of certain preferences. Also, Böhner's experiment had differences in the protocol (for example, he separated parents from offspring at 40 days, not 35 days, thereby increasing the likelihood of learning from the father).

Nevertheless, the situation could be resolved by carrying out one or more of regimes 5 - 11 (Table 4.21). Clearly some are likely to produce more profitable results than others. For example, the three scoring systems all predict a different outcome for regime 8, where a choice is given between learning from the unpaired father or from the male of an unrelated, unfamiliar pair. Also, the scoring systems are based on the assumption that the mother and father exert an equal influence, with regard to tutor choice. A test of this would be to look at the relative preferences for the unrelated male housed with the mother in regime 6 and that

Table 4.21 Predictions of the outcomes of tutoring combinations, using systems whereby scores represent the relative importance of paired status and relatedness

	Tutor choice 1	Tutor choice 2	SYSTEM 1 1	2	Pref.	SYSTEM 2 1	2	Pref.	SYSTEM 3 1	2	Pref.
1.	F + m	U + uf	5	1	F	4	2	F	3	1	F
2.	U_1 + uf	U	1	0	U_1	2	0	U_1	1	0	U_1
3.	F	U + m	2	3	U	1	3	U	1	2	U
4.	F + uf	U + m	3	3	-	3	3	-	2	2	-
5.	F + m	U	5	0	F	4	0	F	3	0	F
6.	F + uf	U + uf	3	1	F	3	2	F	2	1	F
7.	F + uf	U	3	0	F	3	0	F	2	0	F
8.	F	U + uf	2	1	F	1	2	U	1	1	-
9.	F	U	2	0	F	1	0	F	1	0	F
10.	U_1+ m	U_2+ uf	3	1	U_1	3	2	U_1	2	1	U_1
11.	U_1+ m	U_2	3	0	U_1	3	0	U_1	2	0	U_1
12.	U_1+ uf	U_2+ uf	1	1	-	2	2	-	1	1	-
13.	U_1	U_2	0	0	-	0	0	-	0	0	-

Relative importance as cue to song learning:

	System 1	System 2	System 3
Unrelated male	0	0	0
Paired male	1	2	1
Father	2	1	1
Housed with mother	2	1	1

for the father in regime 10. With effects likely to be subtle, large sample sizes in such experiments would be necessary, with perhaps tutoring one young male at a time, to eliminate any possible sibling influences.
What is the relevance of making and testing these predictions about song tutor choice? We already know many of the factors that can influence and direct zebra finch song learning; for example, tutor song structure and perhaps aggression (Clayton 1987b), colour morph (Chapter 2), and the amount and quality of parental care (Eales 1987a, Williams 1990). It is now very clear that many factors may be involved in the choice made by a young male, in his selection of a suitable song model. Rarely will such a bird be faced with a simple choice of two tutors, differing only in a single aspect of relevance to song learning.

This study has considered the preferences that zebra finches have for certain categories of tutor (paired or unpaired, related or unrelated), and how such preferences interact. Many possible causes for the preferences found have been postulated, and further tests are needed to tease them apart. However, it is evident that a variety of cues must be involved in influencing tutor selection, some acting together such that a preference is pushed in the same direction, while others conflict.

If the results of the predictions can be shown to hold true, then it will have been demonstrated that factors such as paired status and the relationship with the tutees, have a combined effect on tutor selection. In other words, the

attractiveness of an adult male as a song tutor results from a variety of factors, which arouse interest and attention from a tutee to varying degrees, and which combine until exposure to that tutor has reached a level at which song learning becomes likely.

CHAPTER 5: SONG TUTOR CHOICE BY ZEBRA FINCHES IN AN AVIARY ENVIRONMENT

5.1 Introduction

From whom do birds learn their songs and on what criteria are such choices made? These apparently straightforward questions have received quite a lot of attention in recent years from ethologists. However, providing complete and satisfactory answers has proved surprisingly difficult in the case of zebra finches.

Work has focussed especially on whether the father's song is most likely to be that copied by young males in the wild (e.g. Immelmann 1969, Böhner 1983, 1990, Eales 1985b, 1987b, Williams 1990, Zann 1990 and Chapter 4 of this thesis), but conflicting conclusions have been reached (Slater and Mann 1990).

Most of the studies investigating the factors that may influence song tutor selection have been carried out in controlled laboratory situations. These have revealed a great deal about why a tutee might learn its song from one adult male, instead of from another. For example, it has been shown that tutor choice can be influenced by morphology (Chapter 2), song characteristics (Clayton 1987b) and by the quality and quantity of certain social interactions, especially those involving parental care (Immelmann 1969, Eales 1987a) and perhaps tutor aggression (Clayton 1987b).

The protocol used in the above studies frequently involved presentation of only unrelated tutors to the juvenile males, from 35 days onwards (at the start of the sensitive phase for song learning). Under such conditions, the song of one of these adult birds, and not that of the father (present before 35 days), would generally be copied. Such an arrangement has been regarded as having some relevance to the natural situation (Clayton 1987b). Immelmann (1962, 1965) reported that wild zebra finches become independent after five weeks and then associate mainly with other juveniles or non-breeding adults; this would suggest that further contact with the parents is quite unlikely.

Nevertheless, until a field study aimed at resolving the problem is undertaken, the question of how long parents and their offspring associate must remain open to doubt. Furthermore, the issue appears crucial to zebra finch song development. If exposure to the parents is prolonged beyond 35 days, then it has been shown that the father's song will usually be copied, in preference to that of an unrelated bird (Böhner 1983, Eales 1985b).

A recent field study by Zann (1990), in south-west Australia, demonstrated that the fathers' songs might well have been copied directly by young zebra finches; however, it was also possible that unrelated males were being chosen as models, if a preference exists (as found by Clayton 1987b) for tutors with similar songs to those of the fathers.

Zann's results certainly provide a clearer picture of the outcome of zebra finch song learning, although how a tutor is ultimately chosen in the wild will remain a difficult problem to solve, especially because the species is a small passerine that tends to occur in large, nomadic flocks. In contrast, the laboratory work mentioned above has successfully isolated some of the possible influences on tutor choice, but it is not easy to extrapolate such findings to the situation in the wild. This is analogous, in some ways, to problems faced by students of bird navigation. Birds have clearly been shown to be able to navigate by using a wide range of cues under certain experimental conditions; however, working out how such (often conflicting) information is integrated and used by migrants is a much more complex issue.

As a compromise between field and laboratory work, with their associated advantages and disadvantages, zebra finch song development can be studied in aviaries. This gives the potential for complex interactions with many conspecifics, while the birds are still sufficiently confined to allow detailed observation of their behaviour.

This approach was used by Williams (1990). In her aviary, 16 young males were reared, and had the option of learning from their fathers or from any of 11 other adult males. She found that there was no general preference for learning the song of the father. The best predictor of tutor choice was the level of interaction (particularly of parental behaviour, such as feeding) with specific adults after the young had

fledged. Interestingly, most juveniles formed a crêche on fledging, and parents seemed to feed young birds within the crêche indiscriminately.

Williams did not observe interactions once the juveniles had reached 40 days of age. The events after this stage are likely to be very important, especially as the sensitive phase for song learning lasts from approximately 35 to 65 days. For this reason, and because the precise conditions within an aviary are likely to affect the social environment of the birds, and hence their song development, I decided to perform a similar study.

In contrast to the procedure used by Williams, I observed birds mostly from 35 to 65 days. Particular attention was directed at the social development of the juveniles - on how long they retained strong associations with siblings and parents, and on the sort of interactions they had with unrelated birds in the aviary. Ultimately the song tutor choice of the young males was looked at, and related to these behavioural aspects and also to tutor characteristics such as pairing status, song output and morphology.

The likely value of this study is in considering how the various, potentially influential factors can interact and contribute to an individual's eventual selection of song model, or models.

5.2 Methods

Aviaries and subjects

This study involved the use of two aviaries, each measuring approximately 3m x 2m x 3m. Both were set up in an identical fashion, such that each housed four established breeding pairs and four single males. Misleading results could easily have been obtained from an aviary if, for example, a tutor was abnormally aggressive to the juveniles; high levels of aggression might lead to him being used disproportionately as a song model (see Clayton 1987b). The repeated design helps to reduce the possible influence of such individual behaviour on the overall results.

The songs of all the adult males were recorded and sonagrammed prior to the experiment, to ensure that they had a normal structure and yet were sufficiently different to allow easy discrimination between them.

In each aviary, two of the breeding pairs and two of the single males were of the chestnut-flanked white morph, while the rest were fawn. Both varieties show the sexually dimorphic features of the species. In restricted laboratory conditions, it has been demonstrated that young males strongly prefer to learn from tutors of the parental colour (using chestnut-flanked white and grey birds - Chapter 2); two morphs were used in the present design to investigate whether such a strong preference occurs where a greater potential exists for tutor-tutee interaction.

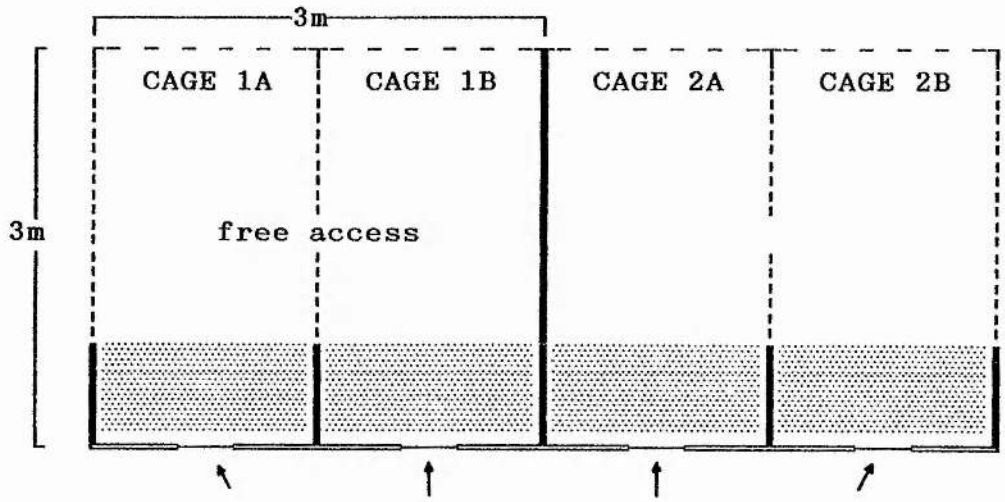
Figures 5.1-5.5 illustrate the structure and design of the aviaries. Each was split into two sections, labelled A and B, between which there was free access. Both aviaries contained 12 nest boxes, approximately 12m of perching and two fir trees. Conditions within the two aviaries were matched as much as possible, by arranging the boxes and perches in a similar fashion.

Mixed seed, grit, nesting material and water, for drinking and bathing, were constantly available. In addition, green food was provided regularly, and egg mixture was supplied when the birds had chicks.

The experiment ran from 5th July 1989, when the breeding pairs were first introduced to the aviaries, through to the first week in November, at which stage all the young had reached 100 days of age. The aviaries were situated outdoors. During inclement weather, birds could take shelter in the trees, or under a roofed section. No artificial lighting was provided.

Breeding in the wild is usually synchronised, because zebra finches usually nest in direct response to rainfall (Immelmann 1962, 1965). To emulate this, six pairs were introduced at first into each aviary. Then, a week later, pairs that were not showing any signs of breeding were replaced. After a further three weeks, the two least synchronous pairs were removed, to leave the required four breeding pairs.

Figure 5.1 Overhead plan of aviaries



▒ - covered area.

¦ - wire mesh "wall"

▌ - solid wall.

Food was provided under the sheltered areas.

FIGURE 5:2 AVIARY C1 : 3-DIMENSIONAL VIEW

Each view is representative of that obtained by looking through the respective observation windows (see Figure 1).

All nest-boxes are labelled.

Note : there was free access between the two cages, through the gap labelled X.

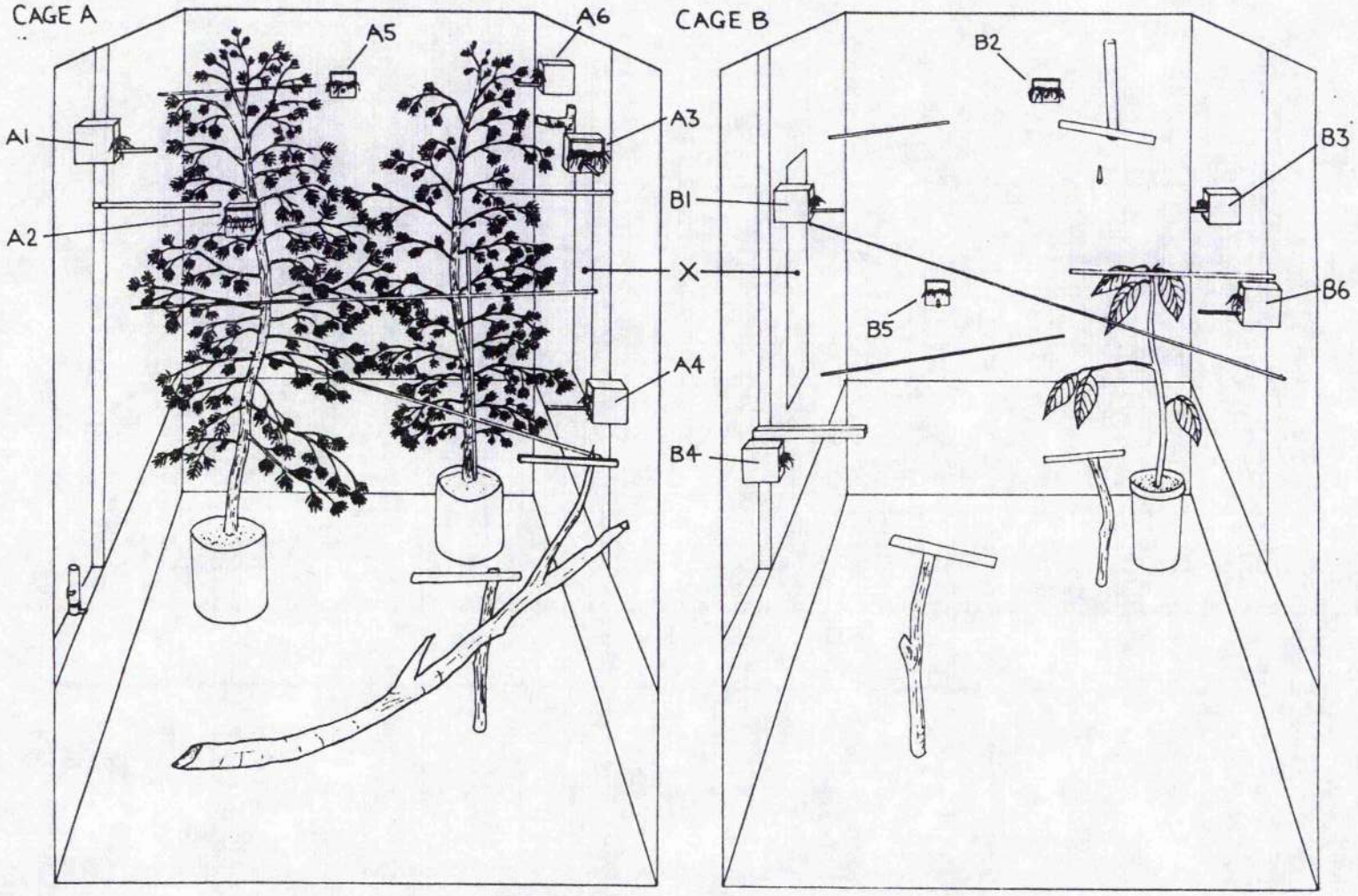


FIGURE 5·3 AVIARY C2 : 3-DIMENSIONAL VIEW

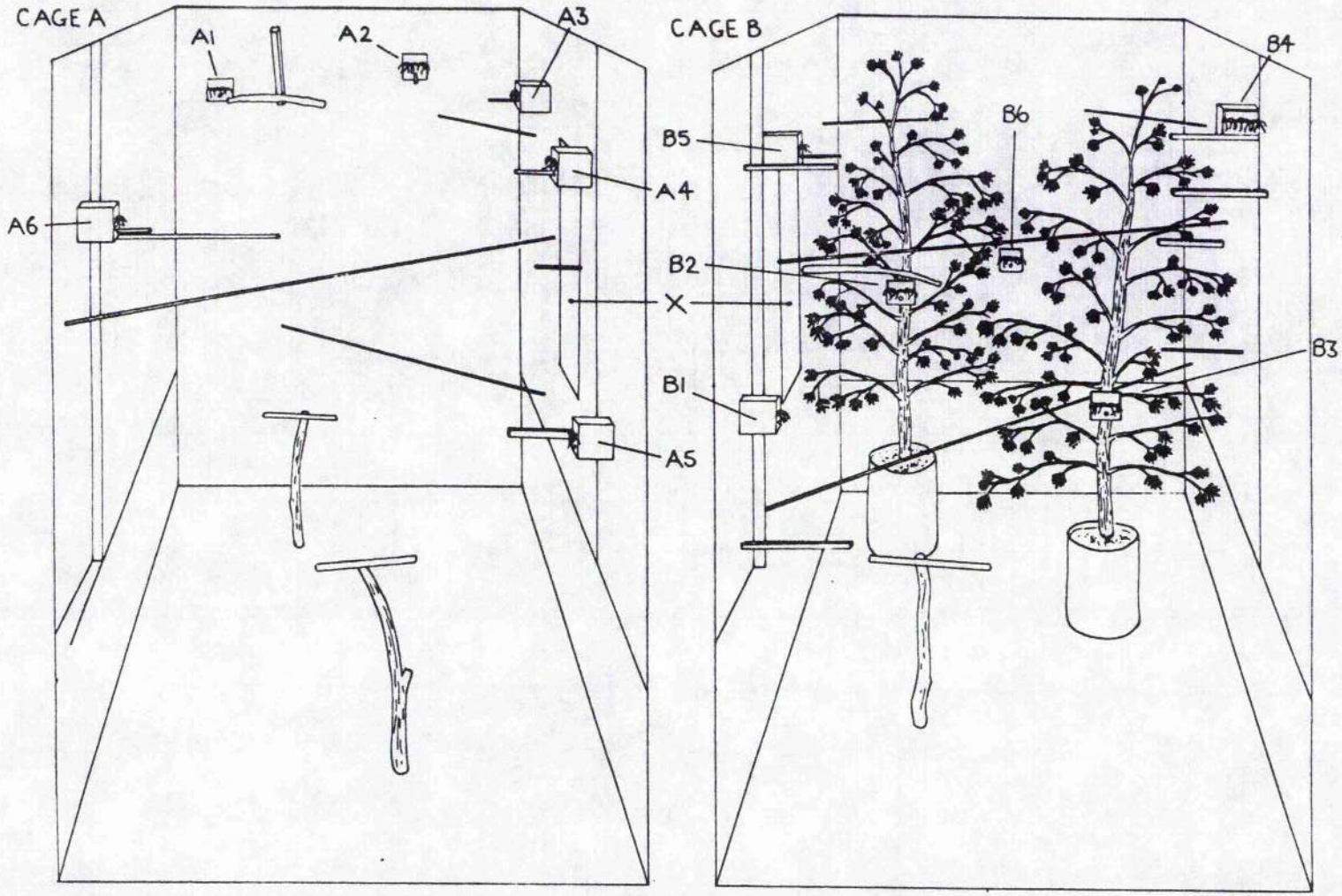


Figure 5.4 View of part of one of the aviaries I

The picture shows three chestnut-flanked white birds, two males and one female (in the middle).

Figure 5.5 View of part of one of the aviaries II

In aviary 1 (C1), 17 young, six of which were male, fledged from the four broods. Eleven days separated the median hatch date of the earliest and latest of these broods. In aviary 2 (C2), 20 young (11 males) fledged, with a hatching span of 14 days. Tables 5.1 and 5.2 give the demographic details for the two aviaries.

It was essential to be able to identify all birds in each cage quickly and accurately. Adults were identified easily by colour rings and plumage characteristics. Whether such rings affected the results of the study is uncertain. Numerous experiments by Burley (e.g. 1986a,b; Burley et al.1982) have shown that ring colour can affect aspects of zebra finch reproductive behaviour. However, any influence on song tutor choice has not yet been shown and, because birds learn their songs, there is less reason to expect an effect (although song copying from individuals with specific ring colours might ensue indirectly because of an influence on social preference). Even if such an effect does exist, it would not necessarily undermine the concept of the experiment; I was looking for direct social and behavioural influences on tutor selection and not so much at *why* a particular individual was, for example, more aggressive or more sexually attractive.

Recently fledged juveniles were more numerous than the adults, were generally less distinctive in their plumage, and had a tendency to clump in groups, all of which made them more difficult to distinguish from one another. Therefore, as well as being colour ringed, each was given

Table 5.1 Demography of aviary C1

Adults	Status	Offspring	Hatch date	35 days	65 days
WOm WOf	Pair 1	W1f W2f W3f W4m W5f W12f	24/7/89	28/8/89	27/9/89
WLGm WRf	Pair 2	F1f F2f F3m W15m	25/7/89	29/8/89	28/9/89
FLGm FLGf	Pair 3	F15m W35f	30/7/89	3/9/89	3/10/89
FOm FOf	Pair 4	F4m W14f W13f W24f F12m	4/8/89 (Died, before observation period)	8/9/89	8/10/89
WDGm	Unpaired				
*WRm	Unpaired				
FDGm	Unpaired				
FRm	Unpaired				

* - died, 26/8/89.

The first letter of each individual identification code represents the bird's colour morph (W: white, F: fawn).

For adults, the following letters represent the colour-ring code (O - orange, LG - light green, DG - dark green, R - red, LP - light pink).

For juveniles, the numbers indicate the dye code (see Figure 5.6)

A bird's sex is indicated by m - male, and f - female.

The median hatch date for each brood is given in the table.

Table 5.2 Demography of aviary C2

Adults	Status	Offspring	Hatch date	35 days	65 days
WOm WOf	Pair 1	W1m W2m W3f W4f W5m	21/7/89	25/8/89	24/9/89
WLGm WLGf	Pair 2	W15f W14m W13m W25m W124f W45f	22/7/89	26/8/89	25/9/89
FRm FRf	Pair 3	F12f F14f F3m F4m F5f	30/7/89	3/9/89	3/10/89
FOm FOf	Pair 4	F15m F1 F13m F2m	4/8/89 Died 7/9/89	8/9/89	8/10/89
WDGm	Unpaired				
WRm	Unpaired				
FDGm	Unpaired				
FLPm	Unpaired				

unique yellow markings using picric acid, on the crown or on the pale underparts (see Figure 5.6). All juveniles were dyed to some extent. There was no evidence that the treatment had an effect on the behaviour or health of the birds. An unfortunate disadvantage of dying feathers as a means of individually marking juveniles, was that remarking became necessary because of the progress of the post-juvenile moult. This inevitably entailed causing temporary disturbance to the aviaries, part way through the period of observations.

The bird density in the aviaries varied from 1.5m^3/bird, when only the adults were present, to 0.56 - 0.62m^3/bird, when all of the juveniles had fledged. In Williams' aviary, the respective values were 0.87m^3/bird and 0.34m^3/bird.

BEHAVIOURAL OBSERVATIONS

Throughout the course of the study regular checks were made on nest boxes, to assess breeding progress. The pair associated with a particular box were regarded as being the "parents" of any young hatched within. Possible consequences of extra-pair copulations and egg dumping were not considered, although both have been shown to occur in the species (Birkhead et al. 1988). Only one extra-pair copulation (involving cloacal contact) was observed during the experiment, although others presumably occurred. Focal observations on particular adults and juveniles were carried out between 4th September and 3rd October 1989 (see Figures 5.7 and 5.8). Each was of 15 minutes duration.

Figure 5.6 Bird marked with Picric Acid

Patches of yellow dye were painted on the crown, breast or belly so that individual birds within the aviary could be quickly and easily identified. This bird is a female of the chestnut-flanked white morph.

Figure 5.7 Dates of focal observations on birds in C1

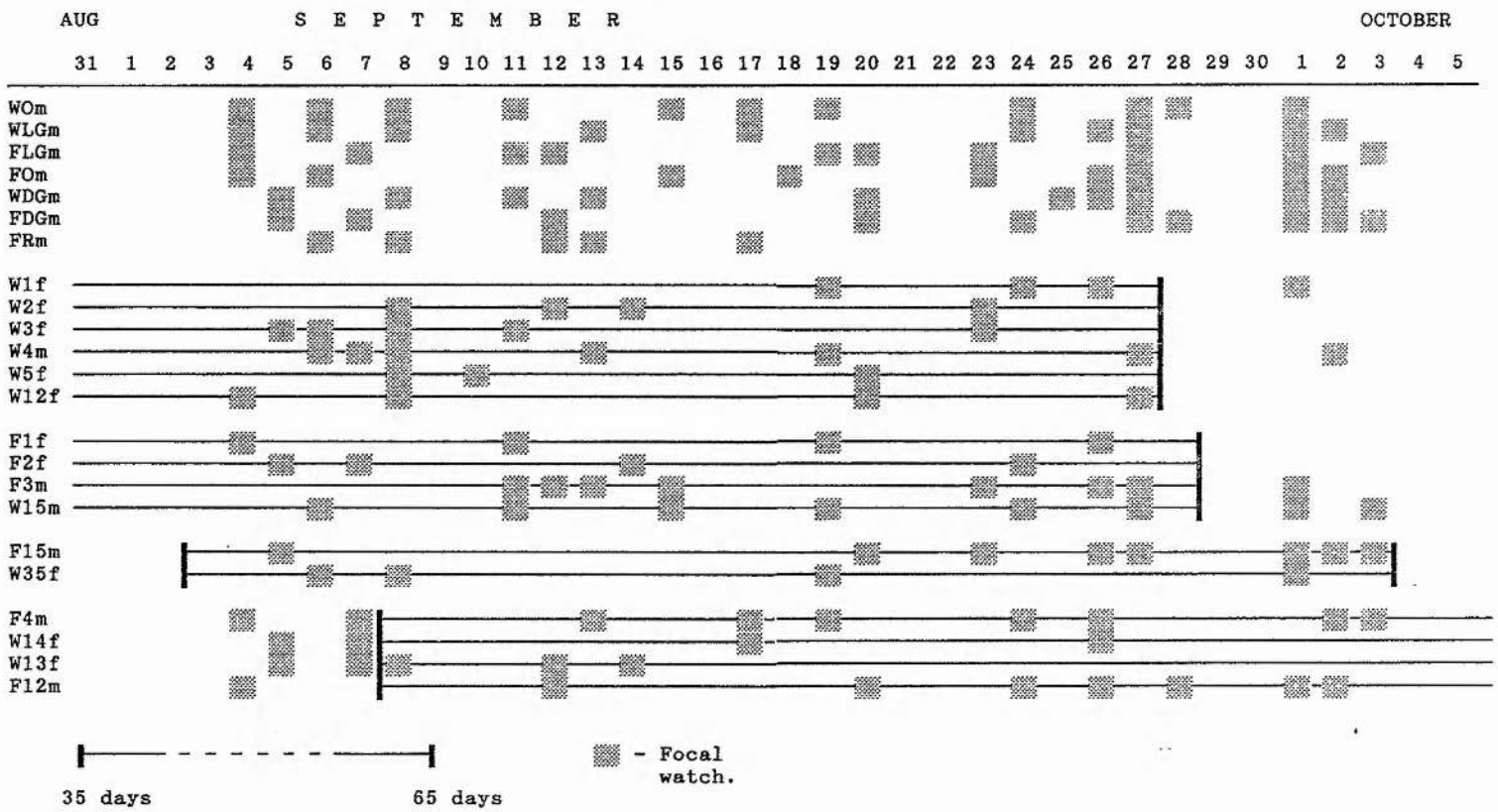
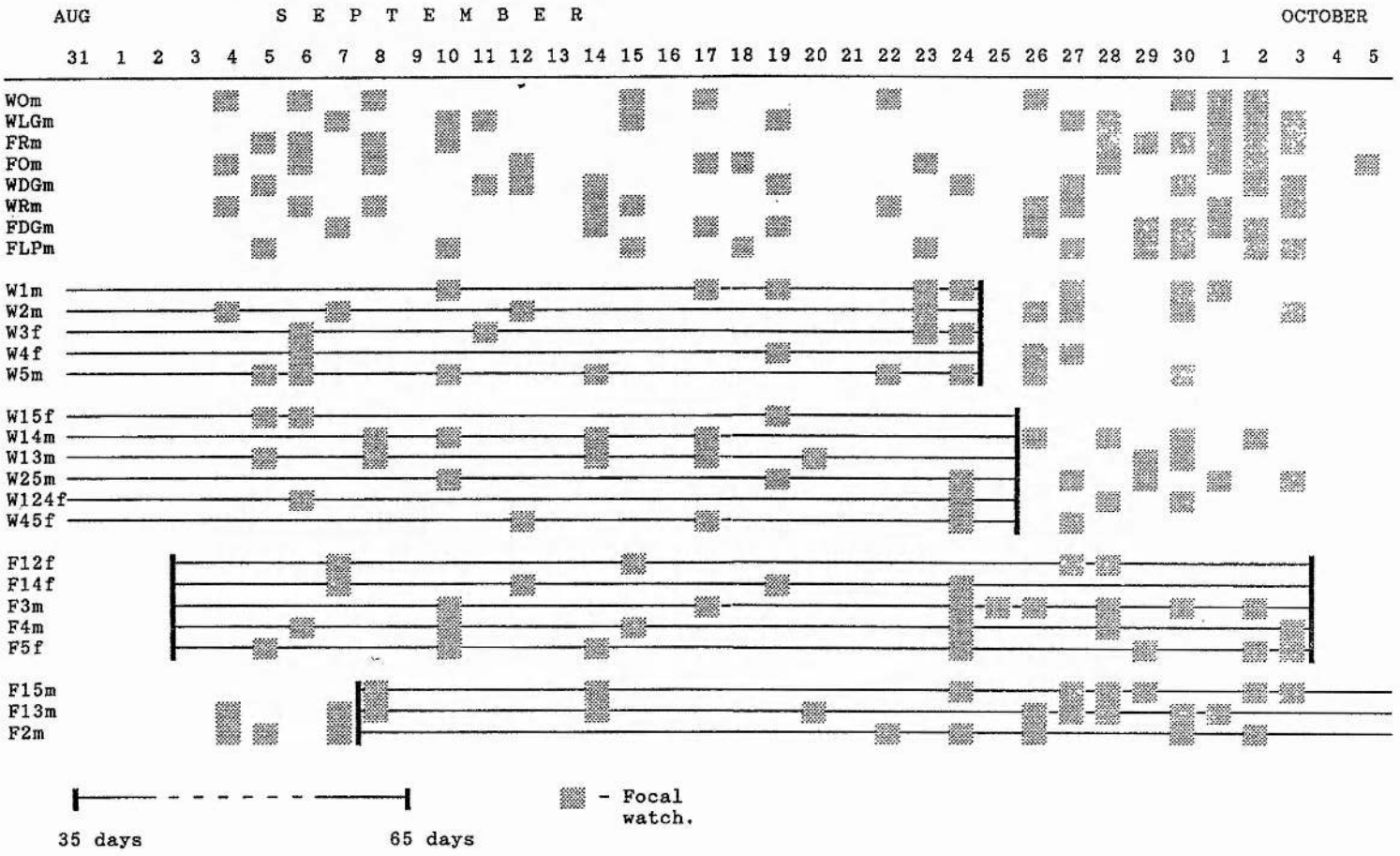


Figure 5.8 Dates of focal observations on birds in C2



Fifteen of the 16 adult males were observed (one unfortunately died shortly after the young had fledged, and was therefore excluded from the analysis), along with 35 offspring. The adult males received 9 - 11 watches each, the juvenile males 7 - 9 and the juvenile females 3 - 5. The observation periods were from 08.30 to 11.00, and from 14.00 to 16.00. Watches for each bird alternated between the morning and the afternoon. Because of the uneven sex ratios in the two aviaries, C2 received nine more hours of observation than C1.

Eighty percent of all juvenile focal watches were made during their sensitive phases; of the remaining 40 watches, 13 occurred during the period 31 to 34 days and 27 were within 66 to 74 days.

Table 5.3 lists the behaviours recorded. Within five "bird-widths" was selected as a suitable range with which to explore the influence of proximity to other birds on song learning. It is equivalent to approximately 15cm. Recording an individual's location within an aviary was possible because all perches were divided by tape into numbered 30cm lengths. Birds could not be so accurately positioned when on the ground, or when in the trees.

SONG RECORDING AND ANALYSIS

On reaching 100 days, the juveniles were taken indoors. Males were housed individually until their songs had been recorded (before 125 days). This was done using a Uher 4000

Table 5.3 Behaviours recorded during focal watches

Behaviour	Recording method
Clumping (with whom?)	I.S. (30)
Birds within 5 bird-widths (which birds?)	I.S. (30)
In nest box (with whom?)	I.S. (30)
Allopreening (with whom?)	one-zero (60)
Feeding (with whom?)	I.S. (30)
Begging (who to, who from?)	one-zero (30)
Feeding of juv. (which?)	one-zero (30)
Aggression (who to, who from, and where?)	counts of all events
Undirected song (number of phrases)	counts of all events
Directed song (who to, number of phrases)	counts of all events
Copulations (with whom, attempted or successful, where?)	counts of all events
Location	I.S (30)

I.S. - instantaneous sampling. Sample interval for this and for one-zero sampling in brackets (in seconds).

Allopreening, begging and the feeding of young were all recorded by one-zero sampling because, although they are not "events", they also do not occur in continuous bouts. It can be difficult, or impossible, to judge objectively whether at any precise moment a bird is engaging in one of these activities.

The "aggression" category was very broad, and included any of the following: supplanting from a perch, pecking and other physical attacks such as chasing, and using the threat call (a distinctive rasping sound) or threat display (bill-pointing or gaping).

Clumping is defined as perching in body contact. This behaviour was not scored when birds were allopreening, which could only occur between clumped birds.

In addition to the above, other behaviours were recorded but not quantified, such as juvenile subsong and nest building.

tape recorder and the songs were analysed using a Kay Digital Sonagraph 7800, following the procedure described in Chapter 2.

5.3 Results

SONG LEARNING ANALYSIS

Table 5.4 shows the pattern of song learning found within the two aviaries. This information is summarised in Table 5.5. The sonagrams used in the analysis and the complete classification of the juveniles' song elements, are shown in Appendices 5.1 and 5.2. The results will be presented in relation to a series of questions.

Did birds learn from single, or multiple, tutors?

Overall, juveniles showed a clear tendency to learn largely from just one adult male. Eight out of the 17 young males copied only from a single tutor. Furthermore, the mean number (± standard deviation) of elements/song copied from the preferred tutor was 7.41 ± 1.91, while 1.65 ± 2.15 were from the second-most preferred, 0.41 ± 0.71 were from other tutors and 1.24 ± 1.03 were unassigned. This strong selectivity for a particular individual emerged despite the fact that two tutors, rather than one, contributed substantially to the songs of three juveniles (W4m and F15m from C1, and W1m from C2).

Table 5.4 Song tutor choice in the two aviaries

C1

Source of elements:

Juvenile	WOm (6)	WLGm (9)	WDGm (9)	FLGm (12)	FOm (10)	FDGm (7)	FRm (11)	Unknown origin
W4m	* 0 *	6	**9**	0	0	0	0	2
F3m	0	* **9** *	0	0	0	0	0	2
W15m	0	* 0 *	**9**	0	0	0	0	2
F15m	0	0	**7**	* 6 *	0	0	1	2
F4m	0	0	0	**9**	* 0 *	0	0	0
F12m	0	0	0	**11**	* 0 *	0	0	0

C2

Source of elements:

Juv.	WOm (6)	WLGm (10)	WDGm (6)	WRm (8)	FRm (10)	FOm (9)	FDGm (8)	FLPm (8)	Unknown origin
W1m	* **6** *	0	5	**0**	0	1	0	0	0
W2m	* 0 *	0	**4**	0	0	1	2	1	3
W5m	* **5** *	0	1	0	0	0	0	0	2
W14m	0	* **8** *	0	0	0	0	0	0	2
W13m	0	* **8** *	0	0	0	0	0	0	0
W25m	0	* **8** *	0	0	0	0	0	0	0
F3m	0	0	0	0	* 0 *	**7**	0	0	0
F4m	0	0	0	0	* 0 *	0	1	**5**	2
F15m	0	0	0	0	0	* **9** *	3	2	1
F13m	0	0	0	0	0	* 2 *	1	**7**	1
F2m	0	0	**5**	0	0	* 2 *	0	0	2

* n * - number of elements copied from father.

Figures in bold indicate the largest contribution to the song.

Table 5.5 Song tutor choice in the aviaries: summary table

C1

Brood	Juv.	Parental morph	Principal song tutor	Other tutors copied from
1	W4m	W	WDGm(9)	WLGm(6)
2	F3m	W	**WLGm(9)**	
2	W15m	W	WDGm(9)	
3	F15m	F	WDGm(7)	**FLGm(6)** FRm(1)
4	F4m	F	FLGm(9)	
4	F12m	F	FLGm(11)	

C2

Brood	Juv.	Parental morph	Principal song tutor	Other tutors copied from
1	W1m	W	**WOm(6)**	WDGm(5) FOm(1)
1	W2m	W	WDGm(4)	FDGm(2) FOm(1) FLPm(1)
1	W5m	W	**WOm(5)**	WDGm(1)
2	W14m	W	**WLGm(8)**	
2	W13m	W	**WLGm(8)**	
2	W25m	W	**WLGm(8)**	
3	F3m	F	FOm(7)	
3	F4m	F	FLPm(5)	FDGm(1)
4	F15m	F	**FOm(9)**	FDGm(3) FLPm(2)
4	F13m	F	FLPm(7)	FOm(1) FDGm(1)
4	F2m	F	WDGm(5)	**FOm(2)**

Number of elements copied from each tutor is shown in brackets.

The boxed tutors are the fathers of the respective juveniles.

The pattern of results is similar to that obtained in the study on colour morphs (Chapter 2), where 6.42 ± 2.79 elements were taken from the song of the preferred tutor, 1.37 ± 1.47 were from other tutors and 1.65 ± 1.70 were left unassigned.

Juveniles tended to have longer songs than did the tutors (mean number of elements 10.71 ± 2.93, compared to 8.60 ± 1.84; Mann-Whitney U-test, n = 17, m = 15, U = 334, p = 0.045). This was not due to the presence of more repeated elements in their songs - such elements were not counted separately, apart from on rare occasions where they were present as a similar repeat in the song of the tutor (in which case they were also counted twice for the adult bird).

WAS THERE A GENERAL PREFERENCE FOR LEARNING FROM THE FATHER?

One out of the six birds in C1 and six of the 11 in C2 learnt their songs mainly from their fathers. Given that there were seven potential song models in C1 and eight in C2, the probability that this level of selection of the father occurred by chance is 0.6 and 0.001, for the two aviaries respectively (Table 5.6). This suggests, if only in C2 where there was a larger sample size, that there was indeed positive selection of the father as the song tutor.

However, this is only true if all of the various adult males were equally available as song models. In fact, it is likely that they were not. Fifteen of the 17 juveniles learnt

Table 5.6 Was there a preference for learning from the father?

		Aviary C1		Aviary C2	
		Observed	Expected	Observed	Expected
Preferred tutor	Father	1	0.86	6	1.38
	Other	5	5.14	5	9.62

The table entries are of "number of birds". Only the principal song tutor in each case is being considered here. The expected value is based on the assumption that all adult males in the aviary were suitable as song models.

In aviary C1, the probability of at least one tutee selecting the father by chance is:

$$1 - \binom{6}{6} \cdot \left(\frac{6}{7}\right)^6 = 0.60$$

In aviary C2, the probability of at least six tutees selecting the father by chance is:

$$\binom{11}{6} \cdot \left(\frac{1}{8}\right)^6 \cdot \left(\frac{7}{8}\right)^5 + \binom{11}{7} \cdot \left(\frac{1}{8}\right)^7 \cdot \left(\frac{7}{8}\right)^4$$

$$+ \binom{11}{8} \cdot \left(\frac{1}{8}\right)^8 \cdot \left(\frac{7}{8}\right)^3 + \binom{11}{9} \cdot \left(\frac{1}{8}\right)^9 \cdot \left(\frac{7}{8}\right)^2 + \binom{11}{10} \cdot \left(\frac{1}{8}\right)^{10} + \left(\frac{1}{8}\right)^{11} = 0.001$$

either from their father or from one of the tutors of the parental morph. Where the father was not preferred, eight out of ten selected instead another tutor of the same colour; this was despite there being more tutors of the other morph present in most cases. Furthermore, of the tutors (excluding the father) that juveniles used as a second, third and fourth preference, nine were of the parental morph and only four were of the other colour.

Bearing in mind these results, and the strong influence of morphological imprinting on song learning, demonstrated in Chapter 2, it is best to assume that there was a real avoidance of non-parental morph birds as song models. Therefore, the above probabilities of birds randomly selecting the father as principal song tutor, need to be modified as the adult males of the alternative colour did not represent a fair choice. Considering only the father and tutors of the same morph as being viable song models, the chance probability of copying mostly from the father is raised to 0.054 (Table 5.7). Although the earlier conclusion, that there *was* a general preference for the father as song tutor, now does not hold statistically, the new result only just fails to be significant.

HOW MUCH DID SIBLINGS INFLUENCE EACH OTHER'S SONG TUTOR CHOICE?

The following is an account of song similarity between sibling males (see also Table 5.8, for summary):

C1 Brood 2. F3m & W15m. No elements in common.

Table 5.7 Was there a stronger preference for learning from the father than for other birds of the same morph?

		Observed	Expected
Preferred tutor	Father	6	3
	Other	6	9

The probability of six, or more, out of 12 juveniles randomly selecting their father as the principal song tutor, calculated by binomial expansion, is 0.054.

In contrast to table 6, here adult males are only considered to have been suitable song models for juveniles, if they were of the same colour morph as the parents.

Data from aviaries C1 and C2 were combined for the analysis, in the case of juveniles that had an effective choice of four song tutors. This excludes the young birds from C1 that had white parents (one of the white tutors had died).

Also excluded were F15m from C1 and F2m from C2. These individuals evidently did not restrict themselves to a tutor choice based on only parental morph birds, as their preferred tutors were of the alternative colour.

Table 5.8 Song similarities amongst sibling pairs

Aviary	Brood	Sibling dyad	Same preferred tutor?	N°. of shared elements
C1	2	F3 - W15	NO	0 (-)
C1	4	F4 - F12	YES	9 (1)
C2	1	W1 - W2	NO	5 (2)
C2	1	W1 - W5	YES	5 (1)
C2	1	W2 - W5	NO	0 (-)
C2	2	W14 - W13	YES	8 (1)
C2	2	W14 - W25	YES	7 (1)
C2	2	W13 - W25	YES	7 (1)
C2	3	F3 - F4	NO	0 (-)
C2	4	F15 - F13	NO	5 (3)
C2	4	F15 - F2	NO	1+ (1)
C2	4	F13 - F2	NO	0 (-)

In brackets - the number of tutors contributing to the shared elements.

C1 Brood 4. F4m & F12m. Both learnt song only from FLGm, copying nine and 11 elements from him respectively. These elements were generally reproduced in the same order as in the tutor's song; changes from the original sequence were not identical in the songs of the two juveniles.

C2 Brood 1. W1m, W2m & W5m. W1 and W5 both showed a preference for the song of their father, while W2 preferred WDGm. Looking in more detail, five elements of the songs of W1 and W2 had a common origin, five were shared between W1 and W5, and none were shared between W2 and W5. The shared elements of W1 and W5 (all copied from the father) appeared in a different sequence in their respective songs. However, the five shared by W1 and W2 were learnt in exactly the same order. Of particular significance is the last of these elements, which was taken from the song of FOm, while the others were all derived from WDGm (and were copied in the original order). Given its position in the song of W2, the probability of the element from FOm occupying an equivalent position in that of W1 is $^{1}/_{12}$, if the block taken from WDGm is considered as a single unit (and therefore unlikely to have been split). However, this does make the assumption that any element can theoretically occupy any position in a song; this may well be unrealistic (see Ten Cate and Slater 1991).

C2 Brood 2. W14m, W13m & W25m. All three learnt only from their father, each copying eight elements from him, with seven or eight shared. The elements all tended to be arranged in the same order as in his song. (This does not imply that the young were influencing each other in their song development; they could all have independently had a

strong preference for the father's song, in which case the sharing of a string of elements would be quite likely).

C2 Brood 3. F3m & F4m. No elements in common.

C2 Brood 4. F15m, F13m & F2m. Each selected a different "preferred" tutor. All learnt at least two elements of their father's song. F15 and F13 shared five elements, copied from three different tutors. F13 and F2 had no elements in common, while F15 and F2 shared at least one.

These results show that siblings do not necessarily learn from the same song models. The similarity of the songs of sibling pairs can be categorised as follows:

1. Few (two or less), or no, shared song elements.
   F3 & W15 (C1), W2 & W5, F3 & F4, F13 & F2, F15 & F2.
2. Several shared elements, copied from the same tutor.
   F4 & F12 (C1), W1 & W5, W14 & W13, W14 & W25, W13 & W25.
3. Several shared elements, copied from more than one tutor.
   W1 & W2, F15 & F13.

The likelihood of a direct sibling influence on song development increases through groups 1-3. Certainly, where no elements were shared between a pair of siblings, a weaker behavioural association between the birds might have been expected. This is considered later.

COMPARISON OF THE SONGS OF NON-SIBLINGS

The following dyads of non-sibling males had several song elements in common (the number shared is given in brackets):

C1 - W4 & W5 (9), W4 & F15 (7), W4 & F3 (6), W15 & F15 (7), F15 & F4 (5), F15 & F12 (5).

C2 - F15 & F3 (7), F13 & F4 (4).

In these cases, the shared elements occurred either in the same order as in the model songs, for each bird of the pair, or the sequence was altered, but in a different manner. There is nothing here to suggest that the common source of elements had to do with anything other than the independent selection of the same song tutor.

However, there were cases in C2 where there is some reason to suspect the existence of an influence between juveniles, on their song development. The song of F2, from brood 4 contained the same five-element string, derived from two tutors, as that shared by siblings W1 and W2. Also, W2 and F4 had in their songs the sequence:

Element 3 (from FLPm) - E4(FLPm)/E1(FDGm) - E2(FDGm).

In both situations, it would seem quite unlikely that such a pattern would have emerged by chance, where elements were being copied from more than one tutor.

ANALYSIS OF THE BEHAVIOUR OF THE AVIARY BIRDS

What close sexual and social bonds occurred amongst the aviary birds?

Good indicators of the existence of strong sexual or social bonds between pairs of zebra finches are nest sharing, and clumping and allopreening (Butterfield 1970). At least one of these behaviours was recorded at some stage in all eight breeding pairs, but between no other adult combinations except for two pairs of males (WDGm and FRm from C1 and WDGm

and FDGm from C2). In both cases the relationship between the two males was of a sexual nature and the birds formed the apparent equivalent of a pair bond (as will be discussed further below). For the purpose of this study a pair bond is defined, adapted from Butterfield (1970), as a "reciprocal mutual attachment between two.....sexually mature organisms such that aggressive tendencies are largely suppressed and sexual ones enhanced".

Between adults and juveniles, such associative behaviours only occurred between parents and their offspring, but with again two exceptions, FDGm and W1f (from C1), and WRm and W4f (from C2). These birds formed pair bonds during the observation period (from approximately 50 and 47 days of age respectively for the females). Paired status was determined independently in these, and other such cases, by observations of sexual behaviour, such as persistent directed song from male to the female, soliciting by the female, copulations and by joint nesting behaviour (nest building and defence, and incubation).

Between juveniles, clumping, allopreening and/or the simultaneous occupation of a nest box were recorded in 53 of the 66 sibling dyads, but between only 25 of 225 non-sibling dyads (chi-squared = 124.5, df = 1, $p < 0.001$). Of these latter 25, between seven and nine cases involved opposite-sexed offspring that ultimately formed pair bonds.

What was the nature of associations between adults and juveniles through the sensitive phase?

Figure 5.9 shows the recorded incidents of behaviours indicative of a strong parent-offspring bond, that occurred during the observation period. It is obvious that by forty days filial associations had almost completely terminated. F4m (from C1) was observed entering the parental nest box with its father on its 46th day, but this was exceptional. The situation that existed before 40 days is less clear. Only four of the eight broods were watched during this time. Of these, juveniles from broods 3 and 4 in C1 (including F4m mentioned above), were occasionally observed socialising closely with their parents.

Did the breakdown of the strong parent-offspring bond, as the juveniles reached independence, mean that subsequent exposure to the parents was no greater than that to other adults (Table 5.9)? In fact, over the period 40 - 65 days there was a strong tendency for birds to maintain greater proximity to their fathers than on average to the other males in the aviary (Wilcoxon matched pairs tests: for male offspring, $n = 17$, Wilcoxon statistic = 102.0, $p = 0.083$; for female offspring, $n = 18$, Wilcoxon statistic = 142.5, $p = 0.014$; for male and female offspring combined, $n = 35$, Wilcoxon statistic = 479.5, $p = 0.002$).

Juveniles did not show such closer proximity to their mothers, either for males, females, or for combined sexes of

Figure 5.9 The persistance of the parent-offspring bond

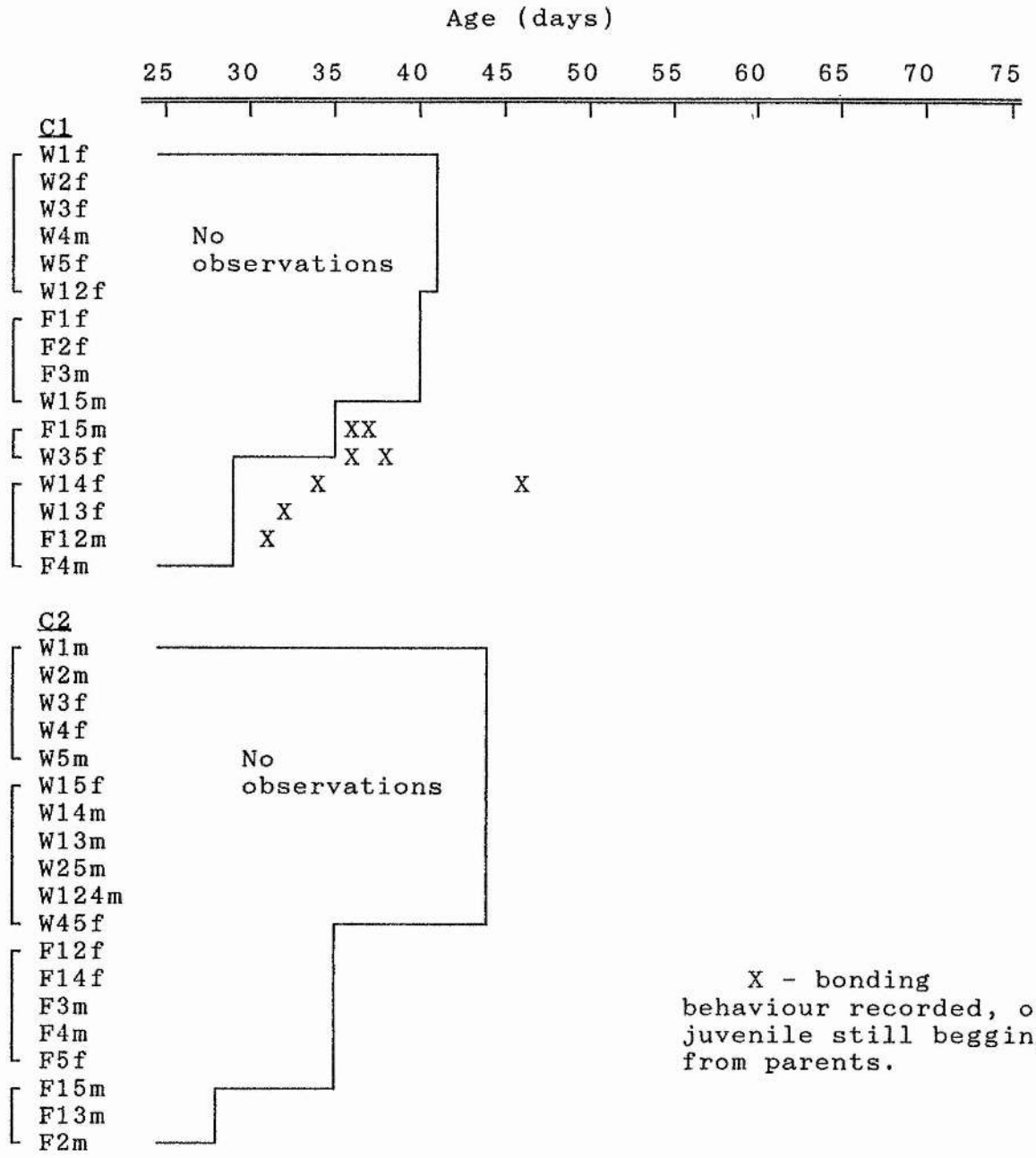


Table 5.9 Proximities of juveniles to their parents and to adults of the parental morph

Proximity to:

Juv. male	F	Om	Om(P)	M	Of	Of(P)	mP	mA
W4	0.9	0.25	0.30	0.0	1.10	0.8	0.30	0.23
F3	0.9	0.10	0.15	0.1	0.07	0.2	0.15	0.08
W15	0.4	0.45	0.55	0.0	0.07	0.0	0.55	0.40
F15	0.4	0.43	0.50	3.0	0.53	0.8	0.50	0.37
F4	0.3	0.26	0.30	0.1	0.43	0.7	0.30	0.23
F12	0.3	0.13	0.20	0.2	0.13	0.0	0.20	0.07
W1	0.2	0.21	0.20	0.8	0.07	0.2	0.20	0.23
W2	0.0	0.17	0.33	0.0	0.27	0.3	0.33	0.05
W5	0.8	0.17	0.27	0.8	0.13	0.2	0.27	0.13
W14	0.8	0.24	0.40	0.0	0.00	0.0	0.40	0.13
W13	1.0	0.24	0.20	0.0	0.13	0.0	0.20	0.28
W25	0.4	0.17	0.30	0.0	0.00	0.0	0.30	0.08
F3	0.2	0.30	0.50	0.9	0.17	0.5	0.50	0.15
F4	0.1	0.27	0.13	0.2	0.17	0.0	0.13	0.38
F15	0.6	0.30	0.30	0.6	0.07	0.1	0.30	0.30
F13	0.5	0.50	0.57	0.3	0.57	1.7	0.57	0.45
F2	0.4	0.46	0.33	0.4	0.27	0.4	0.33	0.55

Proximity to:

Juv. Female	F	Om	Om(P)	M	Of	Of(P)	mP	mA
W1	1.0	0.28	0.15	1.7	0.50	0.7	0.15	0.37
W2	0.6	0.18	0.20	1.0	0.33	0.4	0.20	0.18
W3	0.6	0.18	0.20	0.2	0.07	0.0	0.20	0.18
W5	0.1	0.27	0.50	1.0	0.33	0.5	0.50	0.15
W12	0.9	0.25	0.30	0.0	0.50	1.0	0.30	0.23
F1	0.6	0.20	0.30	0.3	0.43	0.8	0.30	0.15
F2	0.4	0.30	0.25	0.0	0.43	0.5	0.25	0.33
W35	0.8	0.50	0.27	3.3	0.27	0.5	0.27	0.73
W14	0.4	0.27	0.27	0.0	0.17	0.0	0.27	0.27
W13	0.8	0.20	0.13	0.5	0.50	0.0	0.13	0.27
W3	0.1	0.21	0.20	0.0	0.50	0.5	0.20	0.23
W4	0.6	0.18	0.40	1.0	0.00	0.0	0.40	0.08
W15	0.3	0.26	0.10	0.0	0.33	1.0	0.10	0.38
W124	0.4	0.13	0.03	0.0	0.33	1.0	0.03	0.20
W45	0.3	0.31	0.33	0.0	0.53	0.0	0.33	0.30
F12	0.1	0.39	0.53	0.0	0.33	1.0	0.53	0.28
F14	0.6	0.46	0.30	1.7	1.57	3.0	0.30	0.58
F5	0.1	0.23	0.10	0.3	0.67	0.7	0.10	0.33

F - father.
M - mother.

Proximity - samples/focal watch within 5 birdwidths.

Om - mean for other adult males.
Of - mean for other adult females.
Om(P) - mean for other adult males of parental morph.
Of(P) - mean for other adult females of parental morph.
mP - mean for males of the parental morph.
mA - mean for males of the alternative morph.

offspring (probability values from Wilcoxon matched pairs tests were 0.478, 0.925 and 0.568 respectively).

A closer proximity to the father still existed when compared with that to tutors only of the parental morph, but again this only reached significance for combined sexes of offspring and for females considered separately (Wilcoxon matched pairs tests: for male offspring, n = 17, Wilcoxon statistic = 86.0, p = 0.148; for female offspring, n = 18, Wilcoxon statistic = 127.0, p = 0.018; for male and female offspring combined, n = 35, Wilcoxon statistic = 420.0, p = 0.004).

If the father is excluded there is an indication that juvenile males, but not juvenile females, maintained a closer proximity to other adult males of the parental morph, than to those of the alternative colour (Wilcoxon matched pairs tests: for males, n = 17, Wilcoxon statistic = 106.0, p = 0.052; for females, n = 18, Wilcoxon statistic = 62.5, p = 0.523).

<u>What was the nature of juvenile associations through the sensitive phase, both between siblings and between unrelated birds?</u>

Table 5.10 shows, for each individual, a measure of the time spent by juveniles in close proximity to their siblings and to other young birds, through the period from 40 to 65 days of age. Clearly there was a strong tendency for juveniles to spend more time in close company with their siblings.

Table 5.10 Sibling proximity compared to that between unrelated juveniles in the period 40 - 65 days

	Brood	Juvenile	PROXIMITY SCORE (*) Mean for siblings	Mean for non-siblings
C1	1	W1f	2.5	0.4
	1	W2f	2.5	1.2
	1	W3f	5.5	0.7
	1	W4m	4.1	0.9
	1	W5f	4.5	0.5
	1	W12f	4.7	0.8
	2	F1f	3.3	0.3
	2	F2f	2.8	0.6
	2	F3m	3.7	0.6
	2	W15m	1.7	1.3
	3	F15m	7.0	0.5
	3	W35f	7.0	1.4
	4	F4m	1.8	0.9
	4	W14f	1.0	1.4
	4	W13f	1.0	0.7
	4	F12m	2.1	1.4
C2	1	W1m	4.2	0.6
	1	W2m	4.8	0.8
	1	W3f	4.6	0.3
	1	W4f	3.1	0.6
	1	W5m	4.1	0.3
	2	W15f	2.5	0.4
	2	W14m	3.0	0.4
	2	W13m	2.8	0.6
	2	W25m	2.3	0.6
	2	W124f	2.6	0.4
	2	W45f	2.4	0.6
	3	F12f	2.6	0.8
	3	F14f	1.8	1.5
	3	F3m	3.8	0.9
	3	F4m	3.1	1.2
	3	F5f	3.3	0.9
	4	F15m	2.2	1.4
	4	F13m	2.4	1.3
	4	F2m	1.7	0.8

Using Wilcoxon matched pairs test: n = 35, W = 626.5, $p < 0.001$.

* - The proximity scores are based on the focal watches made on each juvenile. They are calculations of:

$$\frac{\text{Number of samples in which birds within 5 bird-widths}}{\text{Total number of focal watches made on either bird}}$$

Table 5.11 Proximity rankings of siblings and unrelated juveniles for each young bird

	Proximity rank									
	HIGH 1	2	3	4	5	6	7	8	9	LOW 10
W1f	W3*	W2*	W12*	W4*	W35	F2	W5*/F3			
W2f	W15+	W3*	W1*/W12*		W5*	W4*W35		F2	F12	
W3f	W5*	W2*	W1*	W4*	W12*	F4+	F12	W15	F15	W14
W4m	W12*	W14+	W3*	W5*	W1*	W2*	W15	F3	F2/W13/F12	
W5m	W3*	W12*	W4*	W2*	F4+	W15	W1*/F15			
W12f	W4*	W5*	W3*	W2*	W1*	W15	F1	F4	W35	F15
F1f	F3*	F2*	W12	W15*	F12					
F2f	F3*	F1*	W35	W15*	F12	W1/W2		W4/W12		
F3m	F1*	F2*	W15*	W4/F15/F12			F4	W35	W1	
W15m	W2+	F3*	W12	F2*	F1*	W5	W3/W4		F12	W35
F15m	W35*	F3	W14	W12/W15/F12						
W35f	F15*	F12+	F2	W13	W2	W1/W12		W14	F3	
F4m	W3+	F12*	W5	W14*	W12	F3/W35				
W14f	W4+	W13*	F4*	F12*	W12	F15	W15			
W13f	W14*	F12*	F3/W12		W4/W15		W1/W35			
F12m	W35+	F4*	F2	F1	W13*	W14*/F3		W15	W2	W3
W1m	W2*	W5*	W3*/W4*		W45	F5	W15/W13/W14/W124			
W2m	W1*	W3*	W5*	W25	W4*	W45	W15	W14/F3/F4		
W3f	W5*+	W4*	W2*	W1*	F3	W14	W25			
W4f	W3*	W5*	W1*	W2*	F5	W15	W45	F14	F13	
W5m	W3*+	W1*	W4*	W2*	F14	W13	F3			
W15f	W45*	W124*	W25*	W13*	W4	W14*	W2	W1		
W14m	W13*	W45*	W25*	F14	W15*/W124*		W1	W2	W3	
W13m	W14*	F14+	W45*	W15*	W124*	W25*	W1	W5	W2	
W25m	W124*	W2	W15*	W14*	W45*/F14		W13*/F4		W3	
W124f	W25*	W15*	W45*	W14*/F5		W13*	W1	W2		
W45f	W15*	W13*	W14*	W1	W124*	W25*	F14	W2/W4/F13		
F12f	F13	F3*	F5*	F4*	F15	F14*	W1			
F14f	W13+	F13	F15	F3*	F5*	F4*	W25/F2		W5/W14	
F3m	F4*	F12*/F5*		F15	F13	F14*	F2	W3/W13		
F4m	F3*	F13	F15	F5*	F12*	F2	F14*	W2/W25		W1
F5f	F3*	F4*	F12*	F15/F13		F14*	W124	W4	W1	W13
F15m	F3/F4		F13*/F5		F14	F12	W3	F2*	W5	W124
F13m	F12	F4	F15*/F3		F5	F14	F2*	W45	W13	W1
F2m	W14+	F13*/F4		F15*	W45/F14		W3			

* - siblings.
\+ - bird with which sexual pair bond formed.
Birds only included if they were in the ten ranks with respect to their proximity to each juvenile, *and* if their proximity score was above a minimum of 0.5 samples within 5 bird-widths/focal watch.

However, such a presentation of data does not reveal whether *all* juveniles within a brood tended to form a cohesive unit through at least part of the sensitive phase. A strong association with a single sibling for each individual could have led to the result. Table 5.11 shows that this was not the case: for most of the juveniles, the proximity to all siblings was high relative to that to other young birds in the aviary. The main exceptions can be seen to be where a sexual pair bond existed between non-siblings. Also, in C1, siblings W13f and F4m had an unusually weak proximity score. In C2, broods 3 and 4 did not follow the pattern of closer proximity between siblings so well; associations between the two broods seemed to have been about as close as those within each brood.

It has already been stated that clumping, allopreening and joint presence within a nest box, occurred more often between siblings than between unrelated juveniles, over the whole study period. Was this also true strictly within the age period 40 to 65 days, by which time the juveniles may have become quite independent? Figure 5.10 links all dyads of juveniles between which such behaviours were observed. There are 35 links between siblings, with 22 between non-siblings. Of the sibling dyads, 17/35 had an associative score of ≥ 2, while only 4/22 non-sibling pairs showed such close bonding (chi-square = 5.36, df = 1, $p < 0.03$). Of these four non-sibling dyads, three involved birds that had developed sexual pair bonds.

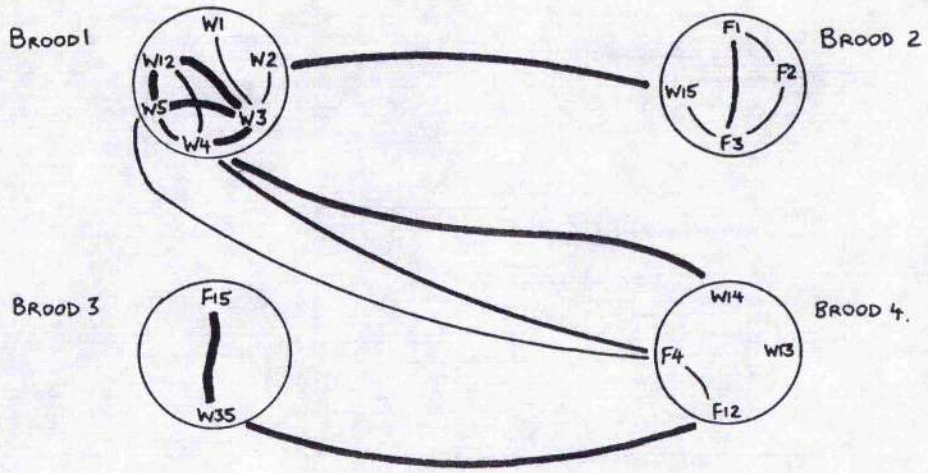
Figure 5.10 Social bonding between juveniles

(legend)

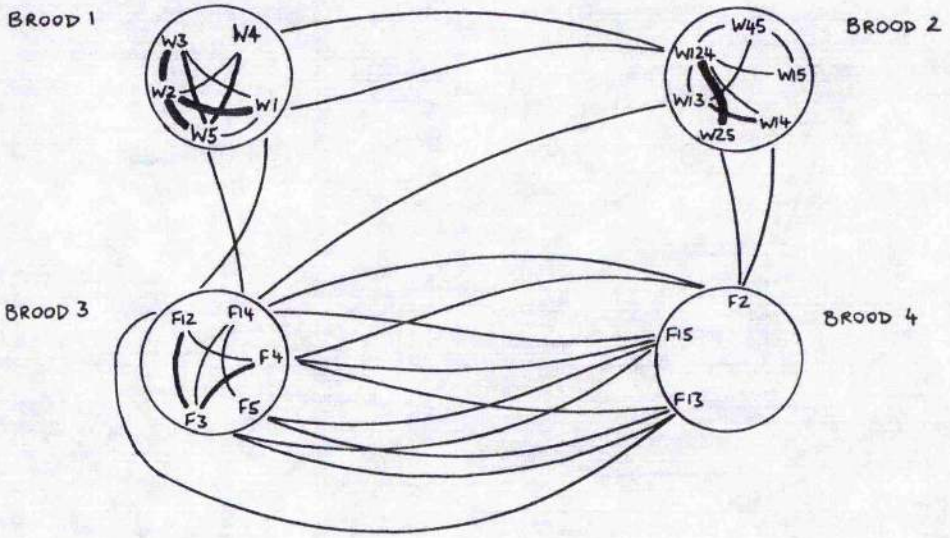
The diagram links those birds between which there was evidence of social bonding (defined here by the occurrence of clumping, allopreening, or their joint presence within a nest box). The relative frequencies of these behaviours were combined for each dyad, to give an overall mean score per focal watch (of instantaneous samples in which they occurred). The behaviours were recorded as exclusive categories (although birds must be clumped for allopreening to be able to occur, in such circumstances only the latter was scored).
The thickness of the line linking two birds corresponds to the the degree of association between them (there are three thicknesses, representing mean scores/watch of < 1, 1-2 and ≥ 2).
In the diagram, members of a brood are enclosed within a circles.

FIGURE 5·10 (see legend).

Aviary C1.



Aviary C2.



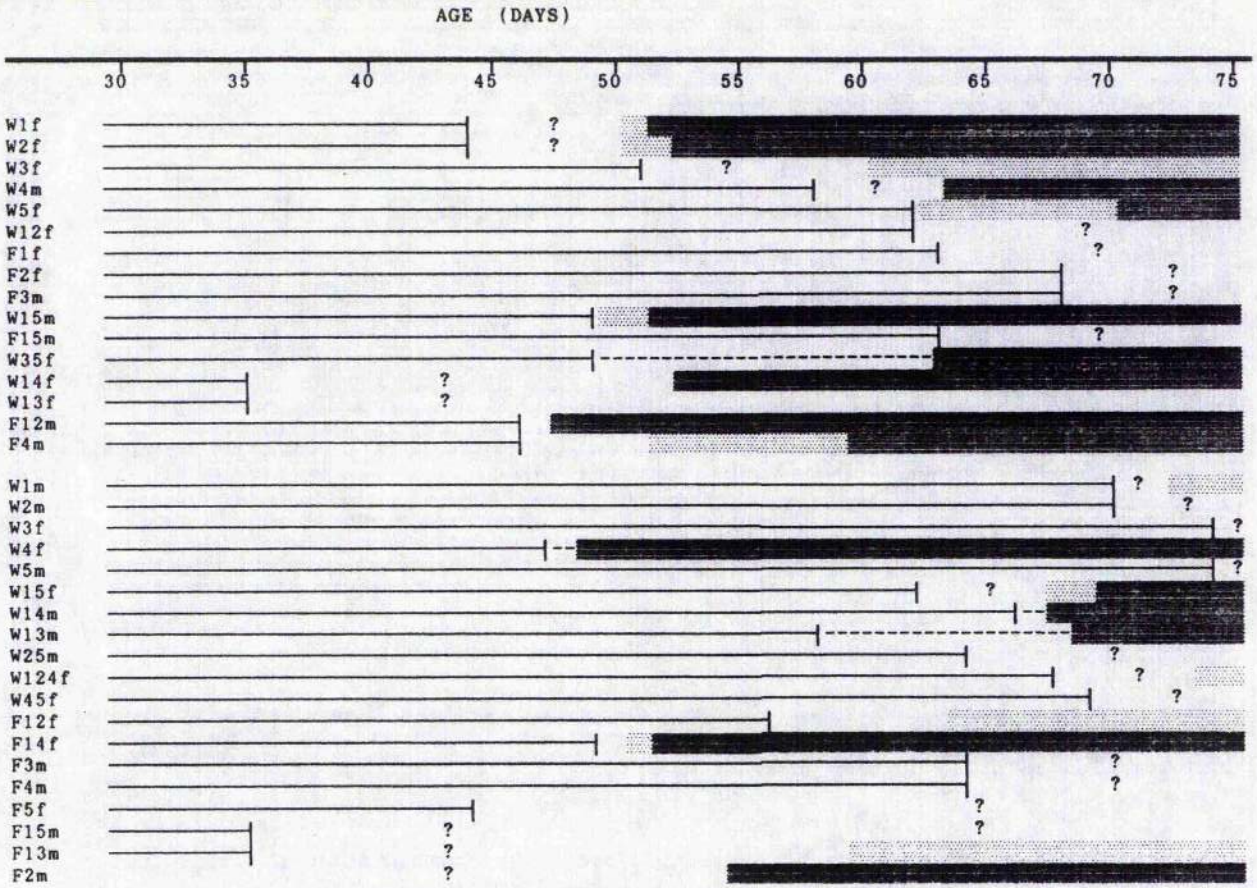
Two broods were atypical (brood 4 from each aviary), in that there was little evidence of close associations between the siblings on the three criteria being measured. Brood 4 in C2 was particularly unusual in this respect, because the juveniles did show such behaviours with birds from brood 3.

There was no evidence for there being a closer proximity between sibling dyads of the same, rather than opposite, sex (using proximity scores for all dyads from the six broods of mixed sex: Mann-Whitney test, $U = 964.5$, $m = 28$, $n = 34$, $p = 0.25$).

Aggression between juveniles was rare. The mean number of agonistic encounters per watch was never higher than 0.6 between any pair of juveniles. Such encounters were observed within 13 of the 66 sibling dyads, and within 80/225 non-sibling dyads (chi-square = 5.90, df = 1, $p < 0.03$), so it appears that aggression was less widespread amongst siblings during the period 40 to 65 days, despite (or perhaps because of) their closer contact with each other.

Figure 5.11 illustrates the approximate ages at which juveniles curtailed their close sibling associations, to form instead sexual pair bonds. These transitions seemed to occur mainly from about 47 days to 70 days. The median date for the onset of pair formation, based on the first day on which clumping, allopreening or nest sharing were observed (only including those birds that did form a pair bond during the study), was 56 days. The actual median date would have been a little before this, because individual birds were not

Figure 5.11 The age of pair formation in the aviaries



———— - period in which bonding with at least one sibling still strong

------- - period in which there was evidence of a continuing sibling bond and also the start of a sexual pair bond.

? - relationships unknown in this period.

▒▒▒▒ - period in which a pair bond had probably been formed.

▬▬▬ - period in which a pair bond had definitely been formed.

The existence of bonding was judged by the presence or absence of clumping, allopreening and nest sharing, and also, in the case of sexual bonds, persistent directed song by the male, solicitation by the female, copulations and any other forms of breeding behaviour.

Although the figure sometimes seems to suggest a very sharp transition between sibling and sexual bonding, little weight should be put on this. The method of data recording was inadequate for the investigation of the nature of such events.

observed daily. It is clear that there was great variation between juveniles. For example, some siblings were not observed engaging in any of the "associative" behaviours beyond 35 days, while others continued to exhibit signs of close social bonding through to 70 days or more (although it should be mentioned that the latest age at which such behaviours were observed, 74 days, occurred between two siblings, W5m and W3f from C2, that appeared to have formed an incestuous relationship).

Table 5.12 lists the pair bonds, involving juveniles, that developed during the course of the observations on the aviaries. Thirteen of the 35 young birds remained unpaired. Three females each paired up with one of the single adult males; interestingly, those males that had a homosexual relationship did not later form a pair bond with young females, when the latter reached sexual maturity.

Nine of the 13 pair bonds that formed involved birds of different morphs. This is not a surprising result, because each individual did not have an even choice, with regard to mate colour morph. For example, in C1, nine white females had only one white male available to them as a potential mate.

Usage of Nestboxes

The nestboxes within each aviary were provided principally for breeding purposes. Half of the breeding pairs moved to a new nesting location after raising their first broods. Their

Table 5.12 Pair bonds that formed within the aviaries

C1

Birds	Date of pairing (day and month)	Age of pairing (if juvenile)
W15m	(12/9) 14/9	(50d) 52d
W2f		(49d) 51d
FDGm	(12/9) 13/9	
W1f		(50d) 51d
F4m	(24/9) 2/10	(51d) 59d
W5f		(62d) 70d
*		
F4m	23/9	50d
W3m		61d
W4m	26/9	64d
W14f		53d
F12m	20/9	47d
W35f		52d

C2

FLPm	(27/9) 29/9	
W15f		(67d) 69d
WRm	6/9	
W4f		47d
W5m	?	?
W3f		
W14m	26/9	66d
F2f		53d
W13m	(19/9) 20/9	(59d) 60d
F14f		(51d) 52d
W1m	1/10	72d
F12f		63d
F13m	3/10	60d
W124f		73d

The following juveniles remained unpaired upto the end of the observation period:

C1 - W12f, F2f, F3f, W13f, F15m, F1f.

C2 - W2m, W25m, W45f, F3m, F4m, F5f, F15m.

(* - F4m appeared to have two mates, W3f and W5f).

success in raising a second brood was not obviously affected by such a decision.

Boxes were also much used as roosting localities, both by juveniles and by non-breeding adults. Once siblings had become independent of their parents, they tended to remain as a cohesive unit (as described earlier), with each brood endeavouring to maintain exclusive access to a particular nestbox. The eight juveniles from broods 3 and 4 (C2) effectively acted as one brood, with regard to site occupation.

During this period of occupation, juvenile "owners" would defend the nest site from other individuals and would spend time collecting and rearranging nest material, or just sitting on, near or within the box.

Regular changes in box occupation occurred, such that whole broods would sometimes move from one site to another. In such times of flux, the process of assessment of suitable new accomodation was often obvious, with birds visiting and entering several boxes in quick succession.

Agonistic encounters

Most agonistic encounters were related to nest-site defence. 66% occurred within 40cm of the nest box of one of the participants. From qualitative observations, it was obvious that the general rule "owner always wins" applied in the area around each nest site. Figure 5.12 shows the decline in

Figure 5.12 The relationship between the likelihood of winning agonistic encounters, and the distance of the encounter from the nest

(legend)

Data for this figure came from: i) encounters that took place at the nest site of one of the participants, and ii) encounters that took place anywhere else in the aviary, as long as the current nest sites of both participants were known at that time, and as long as the distance to the nearest of these sites had been measured.

Nest site "occupancy" was judged by observations of nest building and by persistent presence within the nest (defined here as spending more than two minutes of a focal watch within the nest).

The histogram was built up by amassing the data from all *encounters*; ie. not by taking the mean for each distance, for each separate nesting pair or co-habiting brood. Consequently, there can be no standard deviation bars.

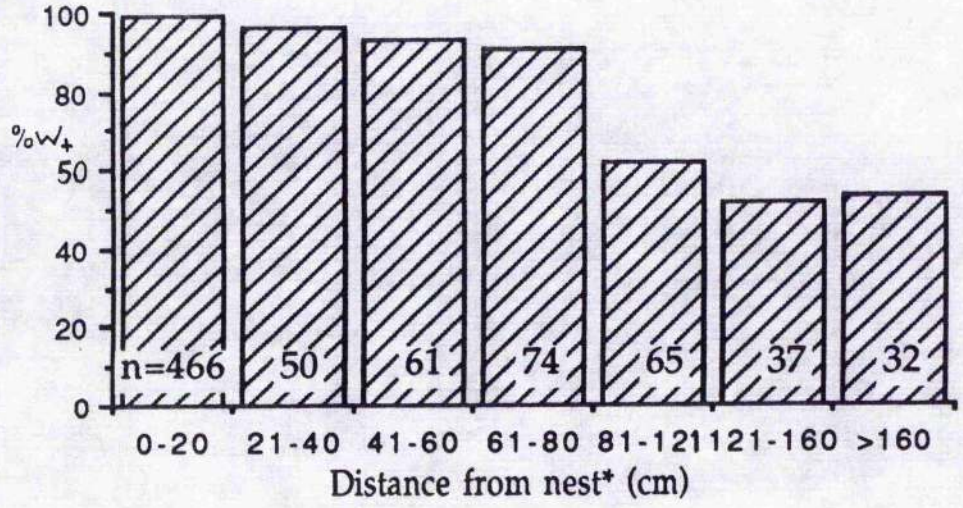
If the sample n for each distance class *is* based on pairs or broods, the standard deviation becomes very large as the distance from the nest is increased. This is because, in most cases, the number of encounters in these locations was usually very small (less than five). Where there was only a single encounter, for example, the "percentage of wins" could only be 0 or 100.

The following table is based, nevertheless, on the proportion of wins, with increasing distance from the nest, calculated separately for each pair or brood:

	Distance from the nest (cm):						
	0-20	20-40	40-60	60-80	80-120	120-160	160+
n	20	11	11	11	19	14	13
Mean % of wins	98.6	95.7	94.0	82.5	50.3	54.6	59.8
S.D.	3.6	10.4	15.3	23.6	40.3	41.3	40.4

Using Mann-Whitney tests, there was no significant difference between groups 0-20, 21-40 and 41-80, or between groups 81-120, 121-160 and 161+. The difference between the first three combined and the second three combined is highly significant (Mann-Whitney test, $n = 46$, $m = 42$, $p < 0.0001$). The % wins for the category 61-80 only bordered on being significantly higher than that of the combined groups with greater distance (MW, $n = 46$, $m = 11$, $p = 0.05$), but was significantly lower than that of the combined groups with a shorter distance (MW, $n = 42$, $m = 11$, $p = 0.007$)

Figure 5.12 (see legend)



+ - % of "wins" in agonistic encounters.

* - distance from nest of participant breeding nearest the location of the encounter.

"n" is the number of encounters, irrespective of which particular birds were involved.

the percentage of wins in encounters, as distance from the nest increased. (Note that this distance is always for that of the participant occupying a site nearest to the point of conflict. Therefore, the low percentage of wins at longer distances was not the result of close encroachment to the nest of the other participant).

Beyond 80cm the percentage of wins dropped to nearly 50%, suggesting that, averaging over all birds, the chance of winning then became random (although some individuals will have continued to win relatively few, or many, encounters depending on their aggression or dominance, etc.). Nearer to a nest than 60cm resulted in the owner winning over 90% of encounters. The situation is less clear between 61 - 80cm; the histogram suggests that there was still generally a very high likelihood of the bird with the nearest nest winning, using data amassed from all encounters. However, this was biased by a few, more aggressive individuals. If the mean percentage of wins, with distance, *of each pair or brood,* are compared, the pattern for 61 - 80cm is not significantly different from that for > 81cm, but *is* significantly less than for 0 - 60cm. This suggests that the transition from winning nearly all encounters, to the random situation, usually occurred within this range of 61 - 80cm.

Courtship and sexual behaviour of the adult males

The amount of directed song by adult males varied from 0 - 25 phrases/hour during the focal watches. This was a significantly lower output than of undirected song (directed

song, mean ± S.D. = 9.87 ± 8.16, undirected song = 53.3 ± 34.9; Wilcoxon matched pairs test, n = 14, W = 103, p = 0.002). Such courtship song (Table 5.13) was not always directed to a bird's mate (but was rarely directed towards juveniles). Of the eight original breeding males, four were observed singing to birds other than their partners. The originally unpaired males sang to a larger number of individuals (for paired males mean number of directed song objects was 1.63 ± 1.51; for unpaired males = 3.57 ± 1.51; Mann-Whitney U Test, U = 44.5, n = 8, m = 7, p = 0.02).

The directed song of paired males was seen only towards females. This was not the case for (heterosexually) unpaired males. The members of a co-habiting male "pair" in each aviary sang to each other. Also two of these four individuals sang both to other males and to females. The partners of these two birds were observed singing only to females, when it was not to the co-habiting male.

A further unmated individual, FDGm from C1, was observed singing to three different males and three females, one of which he later paired with.

Attempted copulations, or successful copulations (i.e. those resulting in cloacal contact), followed a similar pattern (Table 5.13). The males with partners of the same sex copulated with each other. Again, two of them (the same individuals) also attempted to copulate with both other males and females (but were repelled in both situations). Similarly, FDGm attempted, unsuccessfully, to copulate with

Table 5.13 Tutor song performance and copulations

Adult male	Mate	Undirected song rate (*)	Directed song Rate (*)	Who to?	Copulations with: A	S
C1 WOm	WOf	46.8	-	-	-	-
WLGm	WRf	50.0	-	-	-	-
FLGm	FLGf	13.6	24.8	FOf,FOm, F4f	-	FOf
FOm	FOf	-	-	-	FLGf	
WDGm	(FRm)	121.6	14.0	FRm,WOf, WRf	WRf	FRm
FDGm	W1f	64.0	15.2	W1f,WLGm, WDGm,FLGm, FOf,WOf	WDGm,FOf, WLGm	W1f
FRm	(WDGm)	20.8	8.8	WDGm,FLGm, WOf,FOf	-	WDGm
C2 WOm	WOf	94.4	5.6	WOf	-	-
WLGm	WLGf	72.0	4.0	FRf,FOf, F5f	-	WLGf
FRm	FRf	46.0	10.0	FRf,WOf, WLGf WOf	-	-
FOm	FOf	13.2	10.0	FOf,WOf FRf	-	FOf
WDGm	(FDGm)	44.4	24.8	FDGm,FOm, WLGm,FOf	FOm,FOf	FDGm
WRm	W4f	82.0	3.2	W4f	-	W4f
FDGm	(WDGm)	35.6	16.9	WDGm,WOf FOf,FRf	FRf,FOm	WDGm
FLPm	W15f	95.6	10.8	W15f,WOf WLGf,FRf FOf,F5f	WLGf	W15f

* - song rate units : phrase/hour.
Copulations: A - attempted (ie. forced, but resisted).
S - successful (ie. cloacal contact occurred, no apparent resistance from either bird).
"Mate" entered in brackets when there was evidence of a male-male "pair bond".

two other males and one female (other than his mate). The males that had been paired from the onset of the experiment, were involved in fewer incidents of attempted or successful copulations during the observation periods. The only successful extra-pair copulation was between FLGm and the mate of FOm. The mate of FLGm was, at that stage, very ill and the male had been courting the second female vigorously for a few days. At the time of the copulation, this second female solicited strongly to FLGm, but she did not break her pair bond with her original partner.

Tutor song and behavioural criteria and their relationship to song tutor choice

Tables 5.14a and b show various features of tutor song and behaviour. The main choices of song tutors made by juveniles are also shown. Did young males tend to select song models based on any of these aspects?

Across all tutees, the measures of song length, song output, aggression or proximity for the chosen song tutors, were compared using Wilcoxon matched pair tests, to those averaged for the other potential tutors (i.e. those of the parental morph, unless > 2 song elements had been copied from a bird of the alternative colour).

The only measure that proved to be significant in its association with song copying was tutor-tutee proximity (Table 5.15). There was no hint of any relationship between the aspects of tutor aggression considered and song

Table 5.14 Some aspects of the behaviour of adult males, and their interactions with juvenile males

a) Aviary C1

	WOm	WLGm	WDGm	FLGm	FOm	FDGm	FRm
Song length	6	9	9	12	10	7	11
Song output	47	50	136	38	-	79	30
Agonistic encounters:							
Rate(*)	2.4	3.4	2.2	3.8	1.7	4.4	0.9
% wins (A)	92	88	55	58	93	59	11
% wins (D)	100	-	83	-	50	100	-
W4m							
Prox. (1)	0.9	0.5	0.1	0.3	0.0	0.2	0.4
Encounters(2)	0.2	0.1	0.0	0.0	0.0	0.2	0.0
Attacks (3)	0.2	0.1	0.0	0.0	0.0	0.1	0.0
SONG SOURCE		x	X				
F3m							
Prox. (1)	0.2	0.9	0.1	0.1	0.0	0.2	0.0
Encounters(2)	0.3	0.1	0.0	0.1	0.0	0.0	0.0
Attacks (3)	0.2	0.1	0.0	0.0	0.0	0.0	0.0
SONG SOURCE		X					
W15m							
Prox. (1)	0.2	0.4	0.9	0.3	0.2	0.3	0.8
Encounters(2)	0.1	0.0	0.2	0.0	0.1	0.2	0.0
Attacks (3)	0.1	0.0	0.2	0.0	0.1	0.2	0.0
SONG SOURCE			X				
F15m							
Prox. (1)	0.6	0.1	0.4	0.4	0.5	0.2	0.8
Encounters(2)	0.0	0.1	0.0	0.3	0.1	0.1	0.0
Attacks (3)	0.0	0.1	0.0	0.3	0.1	0.1	0.0
SONG SOURCE			X	x			
F4m							
Prox. (1)	0.7	0.0	0.0	0.8	0.3	0.0	0.1
Encounters(2)	0.1	0.1	0.0	0.1	0.1	0.1	0.0
Attacks (3)	0.1	0.1	0.0	0.1	0.1	0.1	0.0
SONG SOURCE				X			
F12m							
Prox. (1)	0.1	0.0	0.1	0.5	0.3	0.1	0.0
Encounters(2)	0.2	0.2	0.2	0.3	0.2	0.2	0.0
Attacks (3)	0.2	0.2	0.2	0.3	0.2	0.2	0.0
SONG SOURCE				X			

Song length - number of elements.
Song output - phrases per hour
* - number of encounters involved in per focal watch.
A - % wins from all encounters, irrespective of location.
D - % wins from encounters occurring at a distance from the nest of greater than 80cm.
1 - mean samples/watch that individuals within 5 birdwidths.
2 - mean number/watch, wins or losses.
3 - mean number of attacks/watch by tutor.

Table 5.14 b) Aviary C2

	WOm	WLGm	WDGm	WRm	FRm	FOm	FLPm	FDGm
Song length	6	10	6	8	10	9	8	8
Song output	100	76	69	85	56	23	106	52
Agonistic encounters:								
Rate(*)	1.4	3.0	3.2	4.1	2.9	2.8	3.7	5.4
% wins (A)	50	60	63	59	93	89	60	67
% wins (D)	-	-	50	38	-	-	-	89
W1m								
Prox. (1)	0.2	0.1	0.3	0.2	0.0	0.5	0.5	0.4
Encounters(2)	0.0	0.2	0.1	0.3	0.0	0.0	0.0	0.2
Attacks (3)	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
SONG SOURCE	X		x					
W2m								
Prox. (1)	0.0	0.4	0.3	0.4	0.0	0.2	0.0	0.0
Encounters(2)	0.0	0.1	0.2	0.1	0.0	0.0	0.0	0.1
Attacks (3)	0.0	0.1	0.2	0.1	0.0	0.0	0.0	0.0
SONG SOURCE			X					
W5m								
Prox. (1)	0.8	0.3	0.2	0.3	0.0	0.0	0.2	0.2
Encounters(2)	0.0	0.1	0.2	0.0	0.1	0.0	0.3	0.1
Attacks (3)	0.0	0.1	0.2	0.0	0.1	0.0	0.3	0.1
SONG SOURCE	X							
W14m								
Prox. (1)	0.4	0.8	0.2	0.6	0.1	0.0	0.1	0.3
Encounters(2)	0.0	0.0	0.1	0.1	0.0	0.1	0.1	0.4
Attacks (3)	0.0	0.0	0.1	0.1	0.0	0.1	0.1	0.3
SONG SOURCE		X						
W13m								
Prox. (1)	0.2	1.0	0.2	0.2	0.7	0.3	0.0	0.1
Encounters(2)	0.0	0.0	0.1	0.1	0.6	0.1	0.1	0.0
Attacks (3)	0.0	0.0	0.1	0.1	0.6	0.1	0.1	0.0
SONG SOURCE		X						
W25m								
Prox. (1)	0.7	0.4	0.0	0.2	0.0	0.2	0.1	0.0
Encounters(2)	0.1	0.1	0.0	0.0	0.3	0.1	0.3	0.0
Attacks (3)	0.1	0.1	0.0	0.0	0.3	0.1	0.0	0.0
SONG SOURCE		X						
F3m								
Prox. (1)	0.3	0.0	0.2	0.1	0.2	0.8	0.4	0.3
Encounters(2)	0.0	0.3	0.1	0.1	0.1	0.0	0.0	0.3
Attacks (3)	0.0	0.0	0.1	0.1	0.1	0.0	0.0	0.3
SONG SOURCE						X		

Table 5.14b continued.

	WOm	WLGm	WDGm	WRm	FRm	FOm	FLPm	FDGm
Song length	6	10	6	8	10	9	8	8
Song output	100	76	69	85	56	23	106	52
Agonistic encounters:								
Rate(*)	1.4	3.0	3.2	4.1	2.9	2.8	3.7	5.4
% wins (A)	50	60	63	59	93	89	60	67
% wins (D)	-	-	50	38	-	-	-	89
F4m								
Prox. (1)	0.2	0.5	0.3	0.5	0.1	0.3	0.0	0.1
Encounters(2)	0.1	0.1	0.1	0.2	0.1	0.1	0.0	0.1
Attacks (3)	0.0	0.1	0.1	0.2	0.1	0.1	0.0	0.1
SONG SOURCE							X	
F15m								
Prox. (1)	0.1	0.3	0.5	0.3	0.5	0.6	0.1	0.3
Encounters(2)	0.1	0.2	0.0	0.1	0.1	0.1	0.0	0.3
Attacks (3)	0.1	0.1	0.0	0.1	0.1	0.1	0.0	0.3
SONG SOURCE						X		x
F13m								
Prox. (1)	0.4	0.3	0.2	0.9	0.8	0.5	0.2	0.7
Encounters(2)	0.1	0.2	0.0	0.0	0.3	0.2	0.2	0.3
Attacks (3)	0.1	0.1	0.0	0.0	0.3	0.2	0.2	0.3
SONG SOURCE							X	
F2m								
Prox. (1)	0.3	0.4	0.8	0.7	0.3	0.4	0.2	0.4
Encounters(2)	0.1	0.2	0.2	0.1	0.1	0.0	0.0	0.5
Attacks (3)	0.0	0.2	0.1	0.0	0.0	0.0	0.0	0.5
SONG SOURCE			X					

Table 5.15 Tutor selection related to tutor song and behaviour

Juv. male	Phrase length (1)		Song output (2)		Aggr.rate (3)		Agg.%wins (4)	
	X	O	X	O	X	O	X	O
W4	9.0	6.0	93.0	47.0	2.8	2.40	1.5	92.0
F3	9.0	7.5	50.0	91.5	3.4	2.30	88.0	73.5
W15	9.0	7.5	136.0	48.5	2.2	2.90	55.0	90.0
F15	10.5	8.6	87.0	41.2	3.0	2.60	56.5	68.6
F4	12.0	9.3	38.0	36.3	3.8	2.30	58.0	54.3
F12	12.0	9.3	38.0	36.3	3.8	2.30	58.0	54.3
W1	6.0	8.0	84.5	76.0	2.3	3.55	56.5	59.5
W2	6.0	8.0	69.0	88.0	3.2	2.83	63.0	56.3
W5	6.0	8.0	100.0	72.5	1.4	3.43	50.0	60.7
W14	10.0	6.7	76.0	84.5	3.0	2.90	60.0	57.3
W13	10.0	6.7	76.0	84.5	3.0	2.90	60.0	57.3
W25	10.0	6.7	76.0	84.5	3.0	2.90	60.0	57.3
F3	9.0	8.7	23.0	69.3	2.8	4.00	89.0	73.3
F4	8.0	9.0	106.0	43.7	3.7	3.70	60.0	83.0
F15	8.5	9.0	37.5	81.0	4.1	3.30	78.0	76.5
F13	8.0	9.0	106.0	43.7	3.7	3.70	60.0	83.0
F2	6.0	8.4	69.0	71.1	3.2	3.33	63.0	68.3

Juv. male	Proximity (5)		Agg.with juv. (6)		Agg. to juv. (7)	
	X	O	X	O	X	O
W4	0.30	0.90	0.05	0.20	0.05	0.20
F3	0.90	0.15	0.10	0.15	0.10	0.10
W15	0.90	0.30	0.20	0.05	0.20	0.05
F15	0.40	0.43	0.15	0.06	0.15	0.06
F4	0.80	0.13	0.10	0.07	0.10	0.07
F12	0.50	0.13	0.30	0.13	0.20	0.13
W1	0.25	0.15	0.05	0.25	0.05	0.10
W2	0.30	0.27	0.20	0.07	0.20	0.07
W5	0.80	0.27	0.00	0.10	0.00	0.10
W14	0.80	0.40	0.00	0.07	0.00	0.07
W13	1.00	0.20	0.00	0.07	0.00	0.07
W25	0.40	0.30	0.10	0.03	0.10	0.03
F3	0.80	0.30	0.00	0.13	0.00	0.13
F4	0.00	0.17	0.00	0.10	0.00	0.10
F15	0.45	0.30	0.20	0.05	0.20	0.05
F13	0.20	0.57	0.20	0.27	0.20	0.27
F2	0.80	0.39	0.20	0.10	0.10	0.10

X - value for selected song tutor. Tutors ignored where ≤ 2 elements copied from them. Mean taken if juvenile had more than one tutor.
O - mean value for other adult males of parental morph (or of either colour, if the juvenile selected a tutor of the non-parental morph).

Table 5.15 continued.

Data analysis: Testing for a difference between values for tutors and values for other males.

Tutor phrase length (1).
Number of song elements.

N	N FOR TEST	WILCOXON STATISTIC	P-VALUE
17	17	106.0	0.170

Tutor song output (2).
Phrases per hour.

N	N FOR TEST	WILCOXON STATISTIC	P-VALUE
17	17	90.5	0.523

Rate of involvement of tutor in agonistic encounters (3).
Mean number of encounters/focal watch.

N	N FOR TEST	WILCOXON STATISTIC	P-VALUE
17	15	70.0	0.589

% of wins by tutor in agonistic encounters (4).
(irrespective of where they occurred).

N	N FOR TEST	WILCOXON STATISTIC	P-VALUE
17	17	57.0	0.368

Tutor-tutee proximity (5)
Mean samples/focal watch that within 5 birdwidths.

N	N FOR TEST	WILCOXON STATISTIC	P-VALUE
17	17	124.5	0.025

Rate of agonistic encounters with juvenile (6)

N	N FOR TEST	WILCOXON STATISTIC	P-VALUE
17	17	76.5	1.000

Rate of attacks on juvenile (7)

N	N FOR TEST	WILCOXON STATISTIC	P-VALUE
17	15	59.0	0.977

learning. It was also intended to consider the percentage of wins by tutors in agonistic encounters occurring only beyond 80cm of their nests (ie. beyond the strong influence of nest site defence). However, too few encounters were observed in such circumstances for these data to be regarded as being representative.

Why did some birds learn from their father, whereas others did not?

Juveniles were categorised as having learnt all (Group 1), some (Group 2) or none (Group 3) of their songs from their fathers (birds were considered not to have learnt from the father where 2 or less elements were copied from him). The groups were examined in relation to the respective phrase length, song output, aggression and proximity of the father, during the period 40 to 65 days (Table 5.16).

Birds that learnt from their father (Groups 1 and 2) did not have fathers with longer songs (Mann-Whitney U test, $U = 75$, $m = 8$, $n = 9$, $p = 0.8$), nor, when considering each individual, did their fathers tend to have songs that were longer than the average for other available tutors (Wilcoxon matched pairs test, $W = 29$, $n = 8$, $p = 0.14$).

The average song output of the fathers of Group 3 juveniles was lower, but not significantly so (Mann-Whitney U test, $U = 89.5$, $m = 8$, $n = 9$, $p = 0.098$) than that for Group 1 and 2 juveniles combined. This tendency was influenced greatly by the case of two Group 3 juveniles, whose father did not

Table 5.16 The degree of copying from the father, related to his song-phrase length, song output, and his aggresion and relative proximity to his offspring

	Juv.	Cage	Phrase length F	Phrase length Others*	Song output F	Song output Others	Aggress. to juv. by F.	Proximity F	Proximity Others
	F3m	C1	9	7.5	50	92	0.1	0.87	0.16
Group	W5m	C2	6	8.0	100	77	-	0.75	0.23
1	W14m	C2	10	6.0	76	85	-	0.78	0.40
	W13m	C2	10	6.0	76	85	-	1.00	0.18
	W25m	C2	10	6.0	76	85	0.1	0.38	0.30
Group	F15m	C1	12	8.7	38	57	0.3	0.44	0.43
2	W1m	C2	6	8.0	100	77	-	0.18	0.19
	F15m	C2	9	8.7	23	71	0.1	0.62	0.33
	W4m	C1	6	9.0	47	93	0.2	0.93	0.32
	W15m	C1	9	7.5	50	92	-	0.36	0.53
	F4m	C1	10	10.0	0	49	0.1	0.29	0.29
Group	F12m	C1	10	10.0	0	49	0.2	0.31	0.17
3	W2m	C2	6	8.0	100	77	-	0.00	0.34
	F3m	C2	10	8.3	56	60	0.1	0.19	0.47
	F4m	C2	10	8.3	56	60	0.1	0.07	0.19
	F13m	C2	9	8.7	23	71	0.2	0.54	0.53
	F2m	C2	9	8.0	23	78	-	0.36	0.42

Group 1 - Birds that copied > 2 elements only from their father.
Group 2 - Birds that copied > 2 elements from their father and also from another male.
Group 3 - Birds that copied > 2 elements only from birds other than their father.

* - value for "others" is mean calculated for tutors of father's morph. However, where birds learnt > 2 elements from a non-parental morph tutor, then the mean was calculated from all other males.

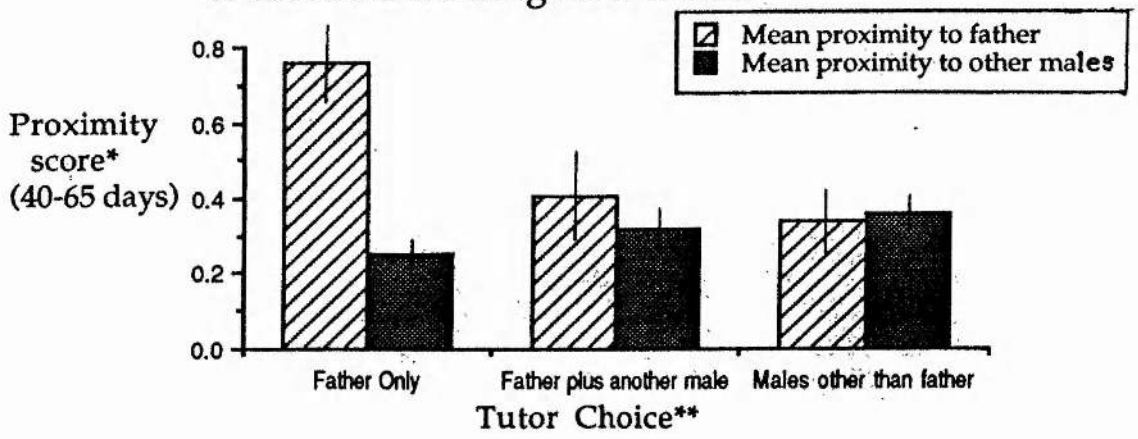
sing at all during focal watches (although he had otherwise been observed singing on at least one occasion).

Aggression to juveniles by their fathers was recorded only at a very low rate, and it is not surprising that the occurrence of such behaviour did not predict the choice of the father as the song model (father to juvenile aggression was seen in four out of eight cases where the father was copied, and in six out of nine cases where he was not).

It has already been shown that close proximity to a tutor is probably, in general, a good indicator of song tutor selection. It is therefore not a surprise that birds learning some or all of their father's song tended to spend relatively more of their time in close proximity to him than did birds that learnt from another male (Mann-Whitney U test, $U = 93$, $m = 8$, $n = 9$, $p = 0.048$; see also Figure 5.13). Birds learning only from their father tended to spend more time in close proximity to him than they did on average to other males of the same morph in the aviary, although the effect was not quite significant (Wilcoxon matched pairs test, $W = 15$, $n = 5$, $p = 0.059$): birds not learning from their father showed no hint of this pattern (Wilcoxon matched pairs test, $W = 13$, $n = 8$, $p = 0.53$).

As well as tending to spend more time in close proximity, was there also evidence that birds learning from their father showed strong filial bonding with their parents for longer? Because such associations (i.e. clumping, allopreening and nest sharing) had almost completely ceased

Figure 5·13 The influence of relative proximity to the father on song tutor choice



* mean samples/watch within five birdwidths (with s.e.)
** tutors only categorised as such if >2 elements copied from them

by 40 days, and as only half of the broods were watched prior to this age, strong statements on the subject are impossible. Certainly there was no striking correlation, as there is evidence that F4m and F12m (C1) were continuing to associate with their parents to 34 days, or even 46 in the case of F4m, yet neither copied from the father: conversely F15m, F13m and F2m from C2 all showed some copying from their father, yet none of the strong associative behaviours were observed between them and their parents after 35 days (when observations on these birds began).

There is a suggestion that rearing a second brood might have reduced the likelihood of copying from the father: 5/8 of the birds with parents that failed to raise a second brood learnt from their father, while only 3/10 birds with double-brooded parents did so. However the effect is not significant (Fisher exact test, $p = 0.19$).

Did siblings that sang similar songs associate more closely with each other than did those that sang different songs?

To test this the proximity scores with each other and with tutors, the time spent in close associative behaviours, and the date at which the sibling association ended, were looked at for each sibling dyad (Table 5.17). Siblings were split into three groups, depending on whether they shared < 2 elements (Group a), several elements all copied from the same tutor (Group b), or several copied from more than one tutor (Group c).

Dyads that made different choices of song tutor did not show a lower overall proximity score than did other dyads (Mann-Whitney U test, n = 7, m = 5, p = 0.57). However, if variation between broods in terms of sibling proximity was large, such effects could have been obscured. Therefore it is useful to look just at broods with three males. W14, W13, W25 (C2) all had a similar number of elements in common. F15 and F13 (C2) shared 5 elements copied from 3 tutors, but had fewer elements in common with their brother, F2. The proximity between F15 and F13 was higher than that between either bird and F2. Similarly W1 and W2 (C2), whose songs shared elements copied from two tutors, maintained a proximity closer than that between W1 and W5 (which shared song elements copied from just one tutor), and closer still than that between W2 and W5 (whose songs shared no elements).

There was no obvious difference between the groups, in terms of tutor proximity within each dyad. For example, where song similarity was high, it might have been expected that a similar pattern of tutor associations would have formed, but this did not seem to be the case (see Table 5.17).

The frequency of associative behaviour did not obviously relate to sibling element sharing. For example, although the highest score was for two Group c birds, W1 and W2 (C2), F15 and F13 on the other hand were not observed clumping, allopreening or nest sharing, despite also sharing elements copied from more than one tutor. Also, W2 and W5 (C2) had

Table 5.17 Sibling song similarity related to their associations

	SIBS.	Cage	Prox. score *	Assoc. score +	Length of assoc.	Most proximate tutors	z
	W15m F3m	C1	2.2	0.5	49	WDG FR WLG WLG WO FDG	0
G	W2m W5m	C2	3.1	2.1	64	WR WLG WDG WO WLG WR	2
R							
O							
U	F3m F4m	C2	4.5	1.2	65	FO FDG FLP WR WLG WDG	0
P							
A	F13m F2m	C2	1.9	-	52	WR FR FDG WDG WR FDG	2
	F15m F2m	C2	1.4	-	52	FO FR WDG WDG WR FDG	1
	F4m F12m	C1	3.2	0.8	46	FLG WO FO FLG FO WO	3
G	W1m W5m	C2	3.7	0.9	64	FO FDG WDG WO WLG WR	0
R							
O							
U	W14m W13m	C2	7.0	1.8	59-60	WLG WR WO WLG FR FO	1
P							
B	W14m W25m	C2	2.0	-	65-67	WLG WR WO WO WLG WR	3
	W13m W25m	C2	1.0	-	59-60	WLG FR FO WO WLG WR	1
	W1m W2m	C2	7.5	5.3	70	FO FDG WDG WR WLG WDG	1
G							
P							
	F15m F13m	C2	2.9	-	59	FO FR WDG WR FR FDG	1
C							

Group A : 0 - 2 song elements shared.
Group B : > 2 elements shared, all copied from the same tutor.
Group C : > 2 elements shared, copied from more than one tutor.
* - Proximity score; amount of time spent within 5 bird-widths, from focal watches between 40 and 65 days.
+ - Association score; the relative amount of time spent clumping, allopreening or nest-sharing (mean samples/watch).
z - The number of the tutors ranked in the top three for each juvenile, in terms of their proximity
Length of association - the last day on which the birds were known to be still associating closely together.

dissimilar songs but showed stronger bonding behaviour than did W1 and W5, which shared several elements.

Similarly, the age up to which strong sibling associations occurred did not relate clearly to song similarity. Some birds associating together throughout the sensitive phase produced totally dissimilar songs. However, if we consider only the two broods containing three males with varying degrees of song similarity, a pattern like that for the proximity data emerges. W1 and W2 (C2), and F15 and F13 (C2), birds which had strong song similarities, were observed clumping, allopreening and nest sharing at an age beyond that observed between the other sibling dyads from within their broods.

Did dyads of non-siblings that sang similar songs associate more closely than those that did not?

Three non-sibling dyads, all from C2 (W2 and F4, W1 and F2 and W2 and F2) shared song features that suggested that they might have influenced each other's song development. However they were not seen clumping, allopreening or nest sharing together, and in the latter two cases the level of proximity from 40 - 65 days, was no higher than the average for that between other male (non-sibling) dyads. The proximity score between W2 and F2 was relatively high compared to that between other male pairs from the same broods, but not higher than that between W2 and F3 (which shared no elements).

No relationship could be found between other aspects of juvenile association and the pattern of song similarity.

5.4 Discussion

Although there were seven or eight adult males in each of the two aviaries, young zebra finches in this study showed a high degree of preference for a single song model. The scale of this bias, towards learning mostly from just one tutor, resembled that found throughout the morph experiment (Chapter 2); this was despite there being considerably fewer tutors available in the latter case. Table 5.18 compares these results, together with those obtained by Williams (1990). In her aviary, she found less copying by each young male from a primary male and correspondingly more from others. It seems likely that the difference was due to the greater bird density (by a factor of approximately two), in her situation compared to that in the present study. This may well have led to the different social organisation that ensued, which will be described shortly, and hence to increased close exposure to a larger number of individuals.

Juveniles tended to have longer songs than those of the adults in the aviaries. This reflects the finding of Williams. In both cases, the cause was *not* that there were more repetitions in juvenile songs. Although the aviary birds, like those in the morph experiment, learnt mainly from one particular tutor, they nevertheless had more

Table 5.18 Tutor selectivity comparison, between present study, the aviary experiment of Williams (1990), and the "morph experiment" (Chapter 2)

	% of song copied from:		
	Preferred song tutor	Other tutors	Unknown origin
Present aviary study	69.2	19.2	11.6
Williams' aviary study(1990)	60.1	30.4	9.5
Chapter 2 (morph experiment)	68.0	14.5	17.5

opportunity to interact with other individuals, so were perhaps more likely to copy a few extra elements. Unassigned elements formed a smaller proportion of the songs of the aviary juveniles, so it would seem that more improvisation was not the reason behind longer songs. Immelmann (1969) and Böhner (1983) commented that wild zebra finches have longer, more complex songs than their captive relatives, and argued that short songs are the consequence of a less stimulating, more impoverished environment.

Was there a preference in the aviary for learning songs from the father? The answer is "probably". The preference bordered on significance, even when it was assumed in the analysis that only birds of the parental morph were available as tutors (certainly there was a tendency to select parental morph tutors above those of the alternative colour). This almost significant relationship resulted despite the exclusion from the analysis of two individuals that copied mostly from a non-parental morph tutor, but which also learnt a substantial proportion of their fathers' songs. These results are in contrast to those of Williams, who claimed that the songs learnt in her aviary more closely resembled those of adult males other than the father.

Rather than attempting to make strong assertions about how these findings might apply to the situation in the wild, it is of more immediate interest to explore why some birds chose their father as the principal song tutor, whereas others did not.

The characteristics of the father's song that were considered seemed to have little effect. No link was found between the number of elements in the song phrase and the likelihood of copying. Clayton (1987b) similarly did not find such a correlation, although in Williams' aviary the same relationship almost reached significance.

Böhner (1983) suggested that the rate of singing would probably only have an influence on song learning if the output was particularly low. Similarly, an apparent avoidance of tutors with a very low song output was reported by Slater et al (1991), in an experiment where tutees were exposed to a series of adult males during the sensitive phase. Such a situation may have occurred in the present study. Birds that copied only from unrelated males had fathers that tended to sing less (but not significantly so). These included two individuals whose father did not sing at all during focal watches.

When considering the correlation between song output and the extent of copying by juveniles, it should be borne in mind that any relationship found might not be causal. A reduced song output, for example, could be an indication of a bird's ill health. Such an individual might actually be avoided as a song model because it is generally less active, rarely interacting with other zebra finches.

When investigating the factors that may have influenced song tutor choice, it is important to consider the social development of the juveniles. Unfortunately, the period

starting immediately after fledging was not covered. Observations started at 30 days at the earliest, but mostly began at 35 days or later, so it was not possible to make strong statements about parent-offspring behaviour during this phase of dependence.

Williams found that adults mostly fed young birds indiscriminately in her aviary. She believed this to be the outcome of juvenile crêching, which would have made it very difficult for parents to identify and feed their own offspring, particularly as the juveniles would beg energetically to any adult. This situation may have had a major effect on the song learning pattern, because there was a strong link between tutor choice and the amount of interaction with adult males during this phase. Fathers did not tend to have closer contact with their sons than did other males, and were not preferentially selected as tutors.

Despite there only being a few days overlap in the period of observation chosen by Williams, and that in the present study, it is still clear that the same situation did not arise. When feeding of offspring was observed in my aviaries, it was always between adults and their own young. Furthermore broods tended to strongly retain their individual identity, with mixing occurring to any extent in only one case. This would suggest that the difference between the song learning pattern in the two studies could well have been a direct consequence of the difference in bird density. Perhaps, in Williams' aviary, the juveniles

were constrained by a lack of space into clumping together in a restricted area.

The strong filial bonds between the juveniles and their parents had terminated completely by 40 days, although one bird was seen nest-sharing with its father on day 46. This breakdown of the parent-offspring bond fits quite neatly with the 35 day independence first implemented by Eales in the design of some of her laboratory experiments.

The later date of nest sharing observed in the case of F4m is not without precedent. Zann (1990) reported two cases where young were still roosting with, and being fed by, their parents at 42 and 49 days, and Immelmann (1962) observed a pair feeding 7-8 week old young. Feeding by the parents in the aviaries in the present study was not observed beyond 35 days; it was not seen in Williams' case beyond 40 days.

The extent of such bonding behaviour through the sensitive phase did not seem to relate to the amount of song copied from the father; however, the lack of observations in the period just after fledging, when such behaviours would have been generally much more common, might mean that such an influence was obscured. Also the method of focal sampling might have resulted in the under-representation of quite rarely occurring but nevertheless significant behaviours, such as allopreening. This could mean that, in some cases, a bond was assumed to have terminated when, in reality, it had not.

Relatively more juveniles whose parents went on to successfully raise a second brood learnt from a male other than the father, although not significantly so. Slater and Richards (1990) reported that, where pairs of zebra finches were allowed to re-nest immediately after raising a brood, the father was less likely to be copied by males from the first brood. This result did not appear to be due to an effect on the song output or the aggression of the father; instead, it may have been related to the overall level of exposure to him, because when breeding was prevented he would, of course, have spent less time in nesting activities.

Zann (1990), studying zebra finches in the wild, found no such effect of re-nesting on song tutor choice. A different result in this case was not particularly surprising, as the laboratory birds were confined with their parents until 35 days and were thus more constrained to interact with their fathers, and then with their tutors, rather than with any other males, during this crucial phase of their development. However, Zann's data do not completely rule out an effect of re-nesting. He found that father-son song matching scores did not differ between the two groups, but the possibility remains that birds with re-nesting parents *did* tend to learn from other tutors, but copied preferentially from ones that had songs that closely matched those of their fathers. Such a possibility would be difficult to detect (Slater and Mann 1990).

Juveniles in the aviaries, even after the cessation of the strong association with their parents (marked by behaviours such as allopreening, clumping and nest-sharing), still tended to maintain a closer proximity to their father than to other adult males. Also the degree of proximity was significantly associated with song tutor selection. Do juveniles in the wild retain such closer contact on average with their fathers during the month following independence? Zann (1990) provides no evidence for this from recapture data, but argues that there are plenty of opportunities for contact at the nesting colony and in feeding and drinking flocks. Also, although Immelmann (1965) stated that young feed independently at five weeks and then join juvenile flocks within the colony, he did not conclude that contact with the parents (or other breeding pairs) necessarily ceased.

After they had become largely independent from their parents, the siblings in the present study remained closely associated with each other. They occupied and defended roosting sites together, were jointly involved in nest maintenance and building and generally retained their brood identity. Aggression was more common between unrelated juveniles than between siblings, largely because of disputes over these roosting boxes.

In the wild, Immelmann observed that when the parents started a second brood, the first-brood juveniles would similarly continue to roost together, either in the natal nest, if the parents had changed site, or in another nest.

Other studies on birds that have demonstrated continuing close associations between siblings after independence from their parents include those by Nicolai (1956, on bullfinches *Pyrrhula pyrrhula*), Hötler (1982, on meadow pipits, *Anthus pratensis*), Edwards (1989, on ospreys *Pandion haliaetus*) and Stamps et al (1990, on budgerigars *Melopsitticus undulatus*). Possible advantages of such prolonged sibling associations may relate, as pointed out by Stamps et al (1990), to finding food, spotting danger, elevating social rank (by combining forces in aggressive disputes) and to later mate choice. Also, in the case of zebra finches, cooperative broods may be more successful in acquiring, and defending, superior roosting sites.

A generally closer proximity between siblings than between non-brood mates continued through much of the sensitive phase. Similarly, clumping and allopreening also continued to occur more often between siblings, except in the case of brood 4 in C2. There was no evidence for there being a sex difference in the extent of sibling associations.

The breakdown of close sibling bonding coincided with pair formation. This happened even before 50 days in at least two cases. Such early pairing-up could partly have been the consequence of persistent courtship from the unpaired adult males in the aviaries. However, it is not completely without precedent, as Immelmann (1965) reported that pair bonds in the laboratory may have formed by eight weeks.

Overall, there was considerable variation in the timing and nature of pairing; some pairs involved two juveniles, and others a juvenile and one of the adults, while several individuals had yet to pair up by the end of the period of observations. One apparent pair bond was formed between a brother and sister. Such incestuous relationships are not the norm in zebra finches (Fetherstone and Burley, 1990).

Despite the proven influence of imprinting on the parents, $^{3}/_{4}$ of all the pairs that formed involving juveniles were between birds of different colour morphs. Although these choices were not independent, being constrained by the availability of potential mates, the result does further demonstrate that a strong underlying preference can be over-ridden.

Some of the sibling males produced songs with characteristics suggesting that they may have had a direct influence on each other's song development. There was some evidence that such birds maintained a closer proximity with each other, and showed bonding behaviours for longer, than was the case with other pairs of male siblings. That this evidence was not particularly strong could easily reflect a deficiency of the data.

All forms of agonistic encounters in the aviaries were grouped together, and were recorded and analysed as a single category. The four most apparent reasons behind such interactions were: i) disputes over access to food (this was rare), ii) attempts at plucking feathers, which are used in

nest lining, iii) rejecting the sexual advances of males, and iv) nest-site defence.

The last of these was by far the commonest cause of aggression. Close approach to an occupied nest was always met with an aggressive reaction. Such intrusion nevertheless occurred often; this was possibly a reflection of a lack of perch space, but usually seemed to be the consequence of birds looking for nest material, or for opportunities to take over possession of a box.

It was found that the box occupier would win nearly all encounters taking place within 60cm of the site, but that beyond 80cm the proportion of wins would drop to an average of about 50%. Do these results imply the presence of well-defined territories i.e. is it likely that individuals perceived specific locations as being strictly within the boundary of a exclusively defended area, in contrast to other locations which were effectively neutral, or within another's territory? The alternative is that the likelihood and vigour of attacks on other birds was a direct function of the proximity to the nest, gradually lessening as the distance increased.

The first possibility would predict a sharp discontinuity in the percentage of wins, as the distance from the nest passes just beyond the territory boundary. Superficially, this appears to be exactly what happened, with the hypothetical boundary being usually between 61cm and 80cm from the nest. However, the pattern may have been misleading, because of an

artefact created by the position of the perches. Perches tended to be located either very close to a nest or, alternatively, quite some distance away (> 80cm). Therefore the jump from a very high percentage of wins down to about 50% might have been sharper than would otherwise have been the case, had there been perches in intermediate positions. Also, if zebra finches really did occupy sharply defined territories, then marking of the boundaries in some way would be expected. There is no evidence of this by any obvious means, such as song.

There was no convincing evidence from this study (or from that of Williams) of any link between tutor aggression and the likelihood of song copying. This contrasts with the correlation found by Clayton (1987b), from a laboratory experiment. In her case, closer confinement perhaps increased the intensity or frequency of aggression. Alternatively, or in addition, the influence of other social factors, that are of importance in directing song learning in a more interactive environment, may have been diminished as a direct result of birds being housed in small cages with few other individuals for company.

The correlation in Clayton's experiment provides no information about cause and effect. It is possible that juveniles were first selecting a song tutor, based on some unknown criteria; this may have led to them closely approaching the chosen tutor and it could have been this that caused the aggressive reaction. However, if this is the correct interpretation, and a general phenomenon, then

persistent close approach by juveniles to their chosen song tutor, and the aggressive response, might have also been expected in the aviary situation. As this did not seem to happen, it is more likely that, in the laboratory, aggression was the cause and not the consequence of tutor choice.

The only aspect of tutor aggression that got anywhere near approaching significance, concerned the percentage of wins by a tutor in its encounters outside the immediate area of his nest site. Data from such interactions are sparse, but if they hint at a genuine effect, then they may be an indication that juveniles learn preferentially from more dominant tutors (although Clayton, 1987b, did not find this); alternatively, it could be the consequence of a song learning preference for other tutor characteristics, linked with such aggression (perhaps general health, body size, plumage characteristics, etc.).

In summary, the following are possible influences on song learning in the aviaries:

1. Firstly there did appear to be a preference for learning from the father, but this was by no means absolute.
2. Where the father was not chosen, the song tutor was usually of the same colour morph.
3. Aspects of song (output and phrase length), and aggression (the number of agonistic encounters a male was involved in and his frequency of winning them) did not seem to increase the likelihood of a bird being selected as a song model.

4. The best correlate with song learning was the amount of time that birds spent within close proximity of each other, throughout the sensitive phase. Again there is a cause and effect problem here - perhaps birds choose a preferred song tutor, and then tend to approach that bird more. This might fit with the observations made by ten Cate (1986a) and Adret (in prep.), on listening behaviour in zebra finches, which suggested that juveniles will apparently actively try to improve the quality of the auditory input from a tutor.

Alternatively, learning song could be a more passive process, the consequence of an existing social preference, or from any other set of circumstances that lead to greater exposure to one bird (and its song) above others. Therefore, if the bond with the parents is extended, then it is most likely to be the father's song that is learnt. Similarly, imprinting on, and the resulting closer association with, birds of a particular colour morph, will lead to an increased likelihood of copying song from a bird of that colour. In the absence of a social preference, learning might be directed towards a particular tutor because some aspect of its behaviour (such as aggression) raises its conspicuousness, thus causing increased attentiveness from the juvenile.

This argument does not presuppose that there is an advantage in copying from a specific category of tutor. There may be no selective pressure towards choosing a specific tutor - perhaps all that is important is that a young zebra finch develops normal species-specific song.

It might well be that the father's song is almost always that copied in the wild, as suggested by Zann (1990). The point being made here, however, is that such a pattern of song learning does not require a functional explanation. Whether this is correct may depend on whether females have a sexual preference for males with particular songs. This has not been proven (although they do have a social preference for birds with songs similar to those of their fathers, Miller 1979a).

SEXUAL BEHAVIOUR IN THE AVIARY

The directed song and copulations observed more often involved the adult males that were originally unpaired, than those that were paired. This is not particularly surprising, as both are behaviours associated with mate acquisition and pair formation.

Five males habitually courted and copulated with other adult males to varying degrees. Four of these comprised two homosexual pairs, which engaged in most of the behaviours occurring between a normal heterosexual pair. These bonds between males were perhaps an artefact of captivity, and the precise conditions that were encountered within the aviary - for example, when they were introduced to the aviary they were placed amongst breeding pairs in suitable breeding conditions, but without "spare" females. However, these particular males did not break up their bonds with each other when the females reared in the aviaries became old enough to start breeding. The other unpaired males *did*

acquire partners at this stage. Walter (1973) argued that male zebra finches might develop male-oriented sexuality when housed for a crucial period of their development in isolation from females (as also argued for Mallards by Schutz, 1965). Whether this might have been so for these males here is not known. Homosexual behaviour in zebra finches was first reported by Morris (1954).

FURTHER CONCLUSIONS FROM THE AVIARY STUDY

This study of social development and song learning in the two aviaries was weakened by the late age of the juveniles at the start of the focal watches. The period immediately after fledging could well have a crucial effect on, for example, whether the father's song will be copied or not. Conversely, the observations of Williams, did not extend far enough into the sensitive phase for song learning. Neither study could therefore hope to provide a complete picture of how juvenile relationships influence song tutor selection in a highly interactive environment.

The present study, in hindsight, might also have revealed more had it involved more regular and thorough observations on fewer individuals. It would then have been possible to track more accurately a bird's developing associations and the changing influences on its behaviour, as it progresses through to maturity.

Of a more specific nature, in the future emphasis could be placed more on relationships with females. It could be that

they have an indirect influence on song development, by affecting male associations (as suggested by the results of Chapter 4). The possibility of a direct influence, as has been shown to occur in cowbirds (West and King 1988) is presently being investigated at St.Andrews (A.Jones and P.J.B.Slater, in prep.).

Further investigation of the correlation between song tutor choice and the proximity of the song models would be of interest. For example, is it the tutor or the tutee that approaches the other most often (this would reveal which bird is most responsible for maintaining the association)? Also, under what circumstances do approaches occur - i.e. do juveniles approach adult males when they are singing, acting aggressively, feeding, engaging in activities such as courtship or nest-building e.t.c.

As a final comment, it should be stressed that studying zebra finch behaviour in an aviary cannot provide more than tentative conclusions about the likely course of song development in the wild. This is emphasised by the different results obtained in this study, and in that of Williams, which were probably due to different bird densities. However the accuracy with which an aviary represents conditions in the field is not the main point. The value of aviary studies is that they permit detailed analysis of how the social organisation, of this highly gregarious bird, *can* influence song tutor choice. This, in itself, is of considerable interest in the study of song development.

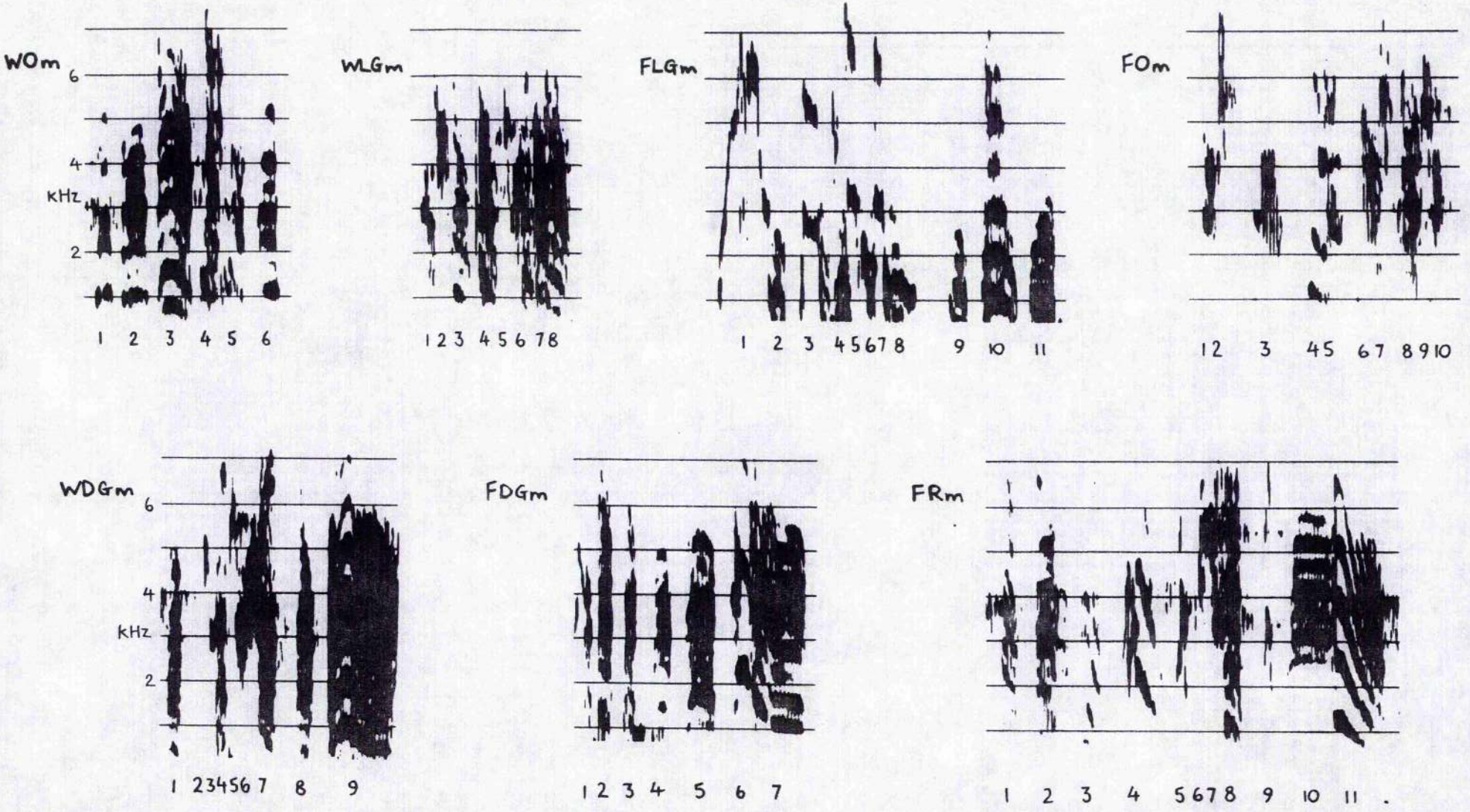
Appendix 5.1 Sonagrams of the birds that were involved in the aviary experiment.

The separate elements within each song are labelled.

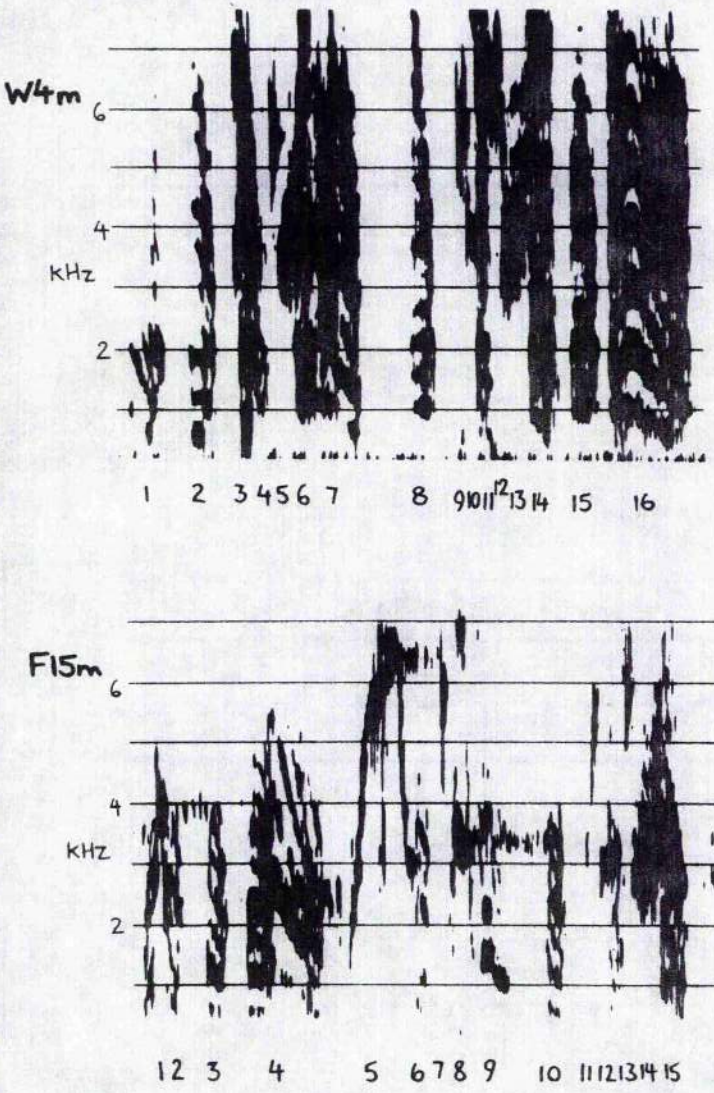
In most cases The noise band upto 500 Hz has been removed.

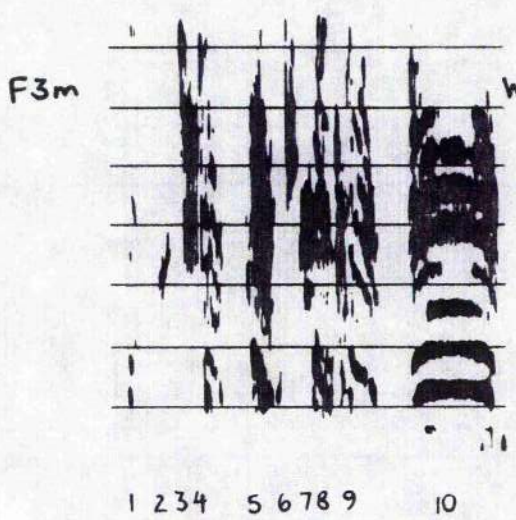
TUTOR AND TUTEE SONAGRAMS.

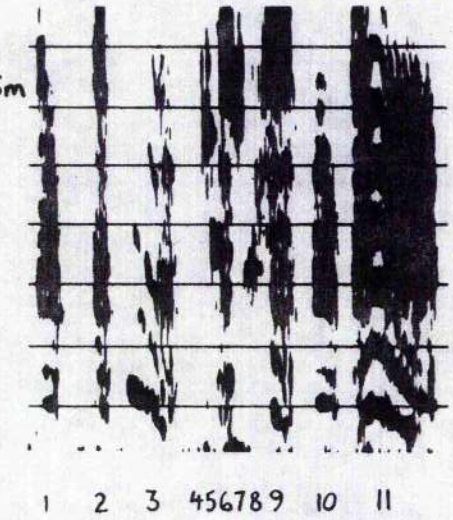
C1 Tutors.

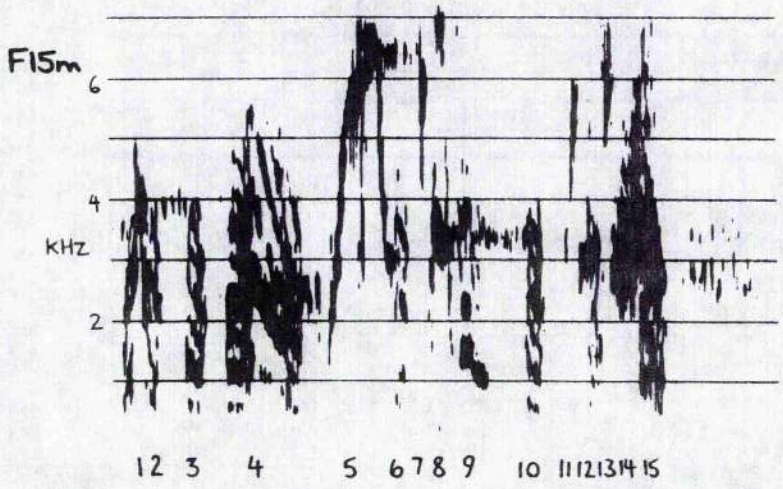


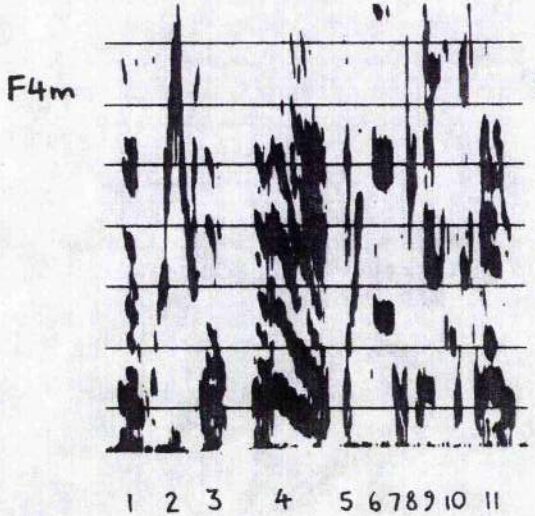
C1 Juvenile males

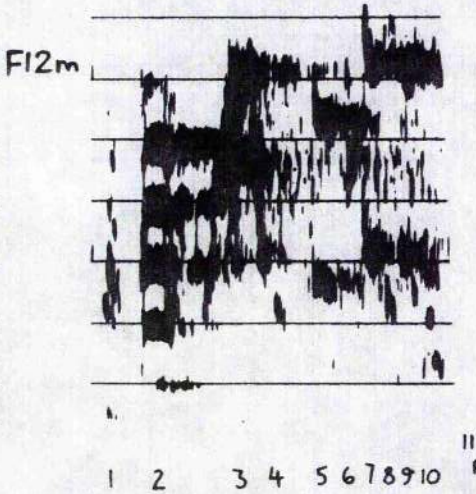






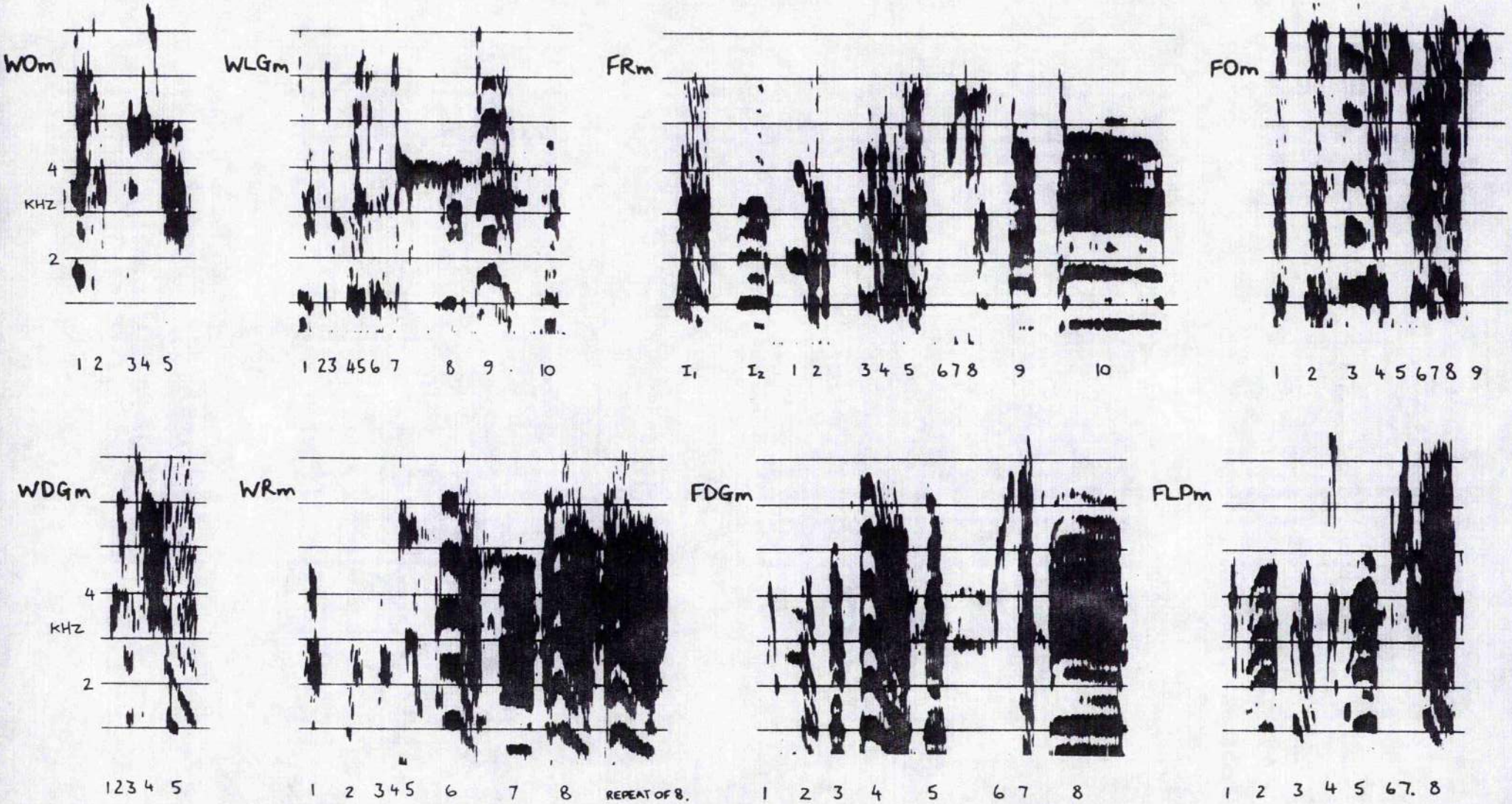




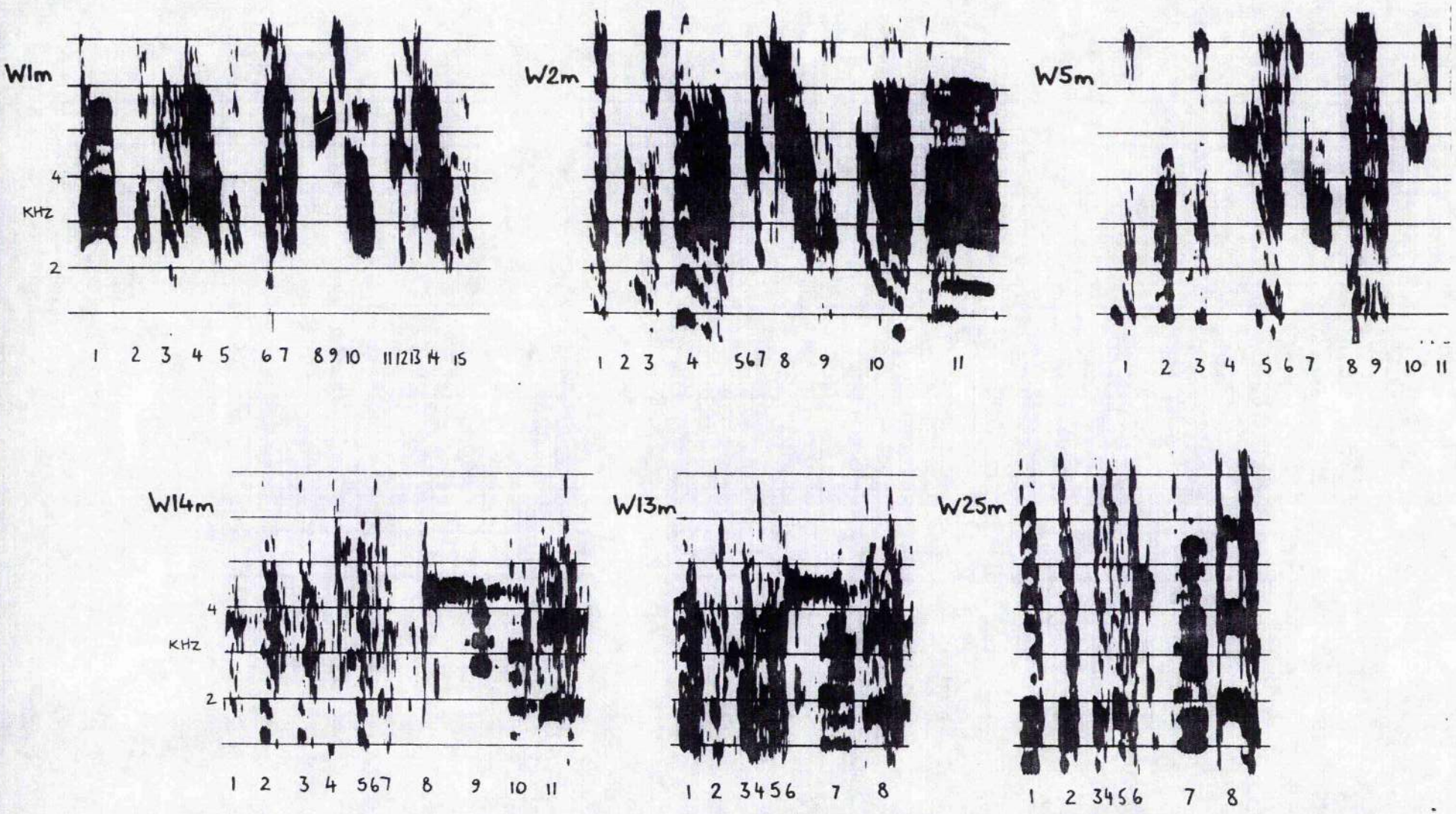


11 NOT PRESENT.

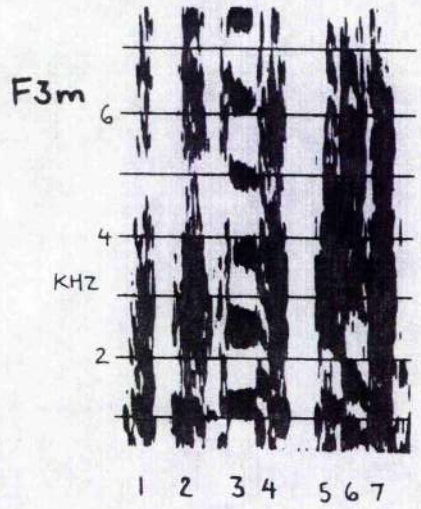
C2 Tutors.

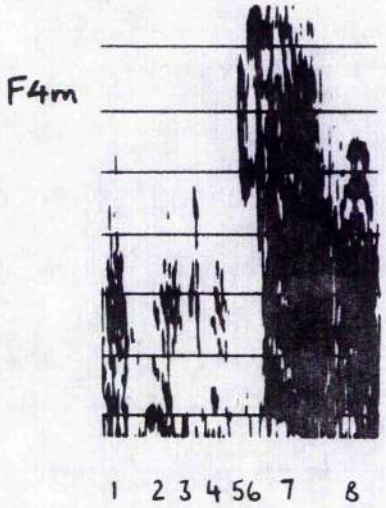

WOm
4
KHZ
2
1 2 34 5
WLGm
1 23 45 6 7 8 9 10
FRm
I1 I2 1 2 3 4 5 6 7 8 9 10
FOm
1 2 3 4 5 6 7 8 9
WDGm
4
KHZ
2
1 2 3 4 5
WRm
1 2 3 4 5 6 7 8
REPEAT OF 8.
FDGm
1 2 3 4 5 6 7 8
FLPm
1 2 3 4 5 67. 8

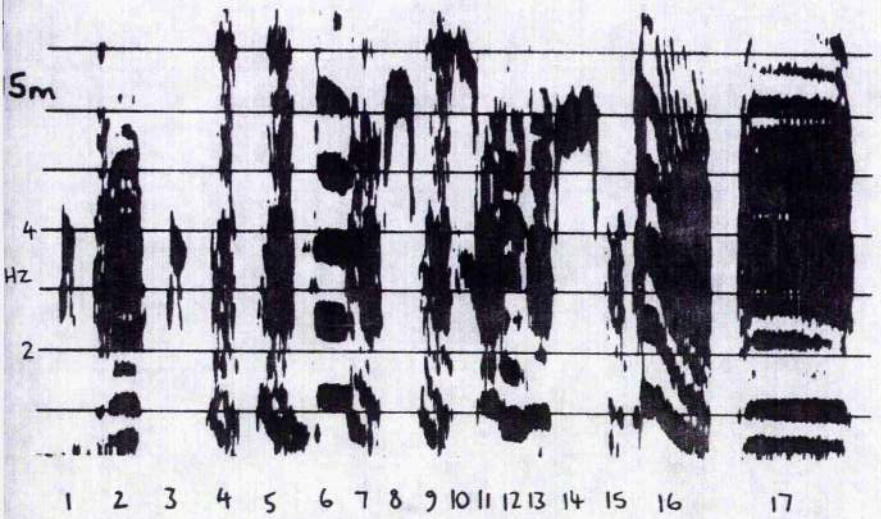
C2 Juvenile males.

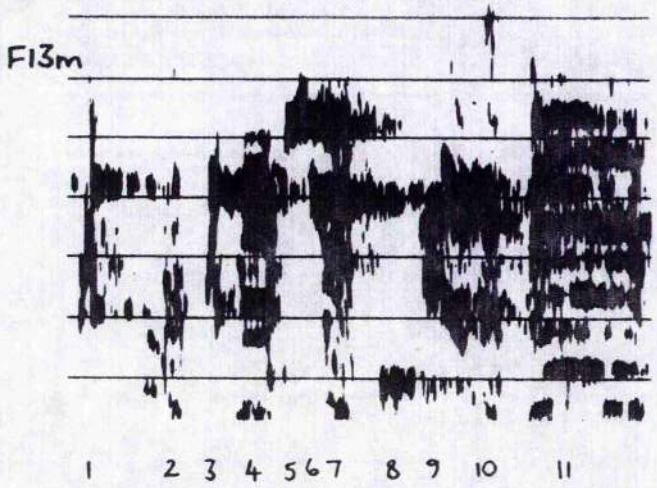


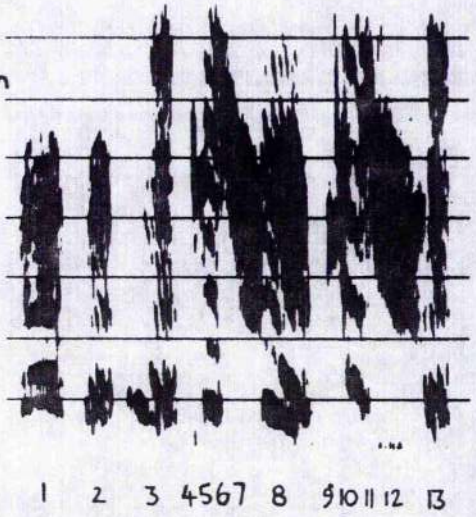
C2 Juvenile males. (continued)











Appendix 5.2 Juvenile song analysis - origin of elements

Note: occasionally a juvenile song element resembled an element from more than one tutor. In these cases, both tutors are listed, with the poorer likeness bracketed. Where a decision could not be made between two tutors, both were bracketed.

The number preceding a tutor's identity code indicates the particular element that had been copied. A blank was left, where an element did not bear a reasonable likeness to any particular tutor element.

AVIARY C1

Juvenile males

	W4m	F3m	W15m	F15m	F4m	F12m
I		$_{1}$2WLGm				
E1:	($_{3}$W15m/$_{4}$FOm)	-	$_{1}$WDGm	$_{5}$FRm	= E3	$_{9}$FLGm
E2:	$_{3}$WLGm	$_{1}$WLGm	($_{2}$W4/$_{3}$WLGm)	-	$_{1}$FLGm	$_{10}$FLGm
E3:	$_{4}$WLGm	$_{2}$WLGm	($_{1}$W4/$_{4}$FOm)	-	$_{2}$FLGm	$_{1}$FLGm
E4:	$_{5}$WLGm	$_{3}$WLGm	$_{2}$WDGm	$_{11}$FLGm	$_{12}$FLGm	$_{2}$FLGm
E5:	$_{6}$WLGm	$_{4}$WLGm	$_{3}$WDGm	$_{1}$FLGm	= E2	$_{3}$FLGm
E6:	$_{7}$WLGm	$_{5}$WLGm	$_{4}$WDGm	$_{2}$FLGm	$_{3}$FLPm	$_{4}$FLGm
E7:	$_{8}$WLGm	$_{6}$WLGm	$_{5}$WDGm	$_{4}$FLGm	$_{4}$FLGm	$_{5}$FLGm
E8:	$_{1}$WDGm	$_{7}$WLGm	$_{6}$WDGm	$_{5}$FLGm	$_{5}$FLGm	$_{6}$FLGm
E9:	$_{2}$WDGm	$_{8}$WLGm	$_{7}$WDGm	$_{8}$FLGm	$_{6}$FLGm	$_{7}$FLGm
E10:	$_{3}$WDGm	-	$_{8}$WDGm	$_{1}$WDGm	$_{7}$FLGm	$_{8}$FLGm
E11:	$_{4}$WDGm		$_{9}$WDGm	$_{2}$WDGm	$_{8}$FLGm	$_{12}$FLGm
E12:	$_{5}$WDGm			$_{3}$WDGm		
E13:	$_{6}$WDGm			$_{4}$WDGm		
E14:	$_{7}$WDGm			$_{5}$WDGm		
E15:	$_{8}$WDGm			$_{6}$WDGm		
E16:	$_{9}$WDGm			$_{7}$WDGm		
E17:	-					

I : introductory element.

E : standard song phrase element.

- : origin of element unknown.

(appendix 5.2)

AVIARY C2

Juvenile males

	W1m	W2m	W5m	W14m	W13m
I					
E1:	$_{I}$WOm	$_{3}$FLPm	$_{I}$WDGm	-	$_{1}$WLGm
E2:	= E15	($_{4}$FLPm/$_{1}$FDGm)	($_{9}$FRm)	$_{1}$WLGm	$_{2-3}$WLGm
E3:	$_{5}$WLGm	$_{2}$FDGm	($_{I}$FOm/$_{5}$FOm)	= E2	$_{4}$WLGm
E4:	= E14	($_{8}$WRm/$_{4}$FDGm)	$_{3}$WDGm	$_{3}$WLGm	$_{5}$WLGm
E5:	= E15	$_{1}$WDGm	= 1	$_{4}$WLGm	$_{6}$WLGm
E6:	$_{1}$WOm	$_{2}$WDGm	$_{4}$WOm	$_{5}$WLGm	$_{7}$WLGm
E7:	$_{2}$WOm	$_{3}$WDGm	$_{5}$WOm	$_{6}$WLGm	$_{8}$WLGm
E8:	$_{3}$WOm	$_{4}$WDGm	$_{1}$WOm	$_{7}$WLGm	$_{9}$WLGm
E9:	$_{4}$WOm	$_{1}$FOm	$_{2}$WOm	-	
E10:	$_{5}$WOm	-	= E4	$_{8}$WLGm	
E11:	$_{1}$WDGm	$_{8}$FOm	= E6	$_{9}$WLGm	
E12:	$_{2}$WDGm				
E13:	$_{3}$WDGm				
E14:	$_{4}$WDGm				
E15:	$_{1}$FOm				

Juvenile males

	W25m	F3m	F4m	F15m	F13m	F2m
E1:	$_{10}$WLGm	$_{1}$FOm	-	$_{4}$FLP/($_{1}$FDG)	1FLPm	$_{I}$FOm
E2:	$_{1}$WLGm	$_{2}$FO$_{m}$	($_{2}$W4/$_{3}$WLGm)	$_{5}$FLPm	$_{3}$FLPm	= E13
E3:	$_{4}$WLGm	$_{3}$FOm	($_{4}$FLP/$_{1}$FDG)	= E1	$_{4}$FLPm	($_{2}$FO/$_{I}$WDG)
E4:	$_{5}$WLGm	$_{4}$FOm	$_{2}$FDGm	$_{1}$FOm	$_{5}$FLPm	-
E5:	$_{6}$WLGm	$_{6}$FOm	$_{6}$FLPm	$_{2}$FOm	$_{6}$FLPm	= E10
E6:	$_{7}$WLGm	$_{7}$FOm	$_{7}$FLPm	$_{3}$FOm	$_{7}$FLPm	= E11
E7:	$_{8}$WLGm	$_{8}$FOm	$_{8}$FLP/($_{4}$FDG)	$_{4}$FOm	$_{8}$FLPm	= E12
E8:	$_{9}$WLGm		$_{2}$FLP/($_{5}$FDG)	$_{5}$FOm	6 FOm	$_{5}$WDG($_{6-7}$FO)
E9:				= E4	7 FOm	$_{1}$WDGm
E10:				-	-	$_{2}$WDGm
E11:				$_{6}$FOm	$_{8}$FDGm	$_{3}$WDGm
E12:				$_{7}$FOm		$_{4}$WDGm
E13:				$_{8}$FOm		$_{1}$FOm
E14:				$_{9}$FOm		
E15:				$_{3}$FDGm		
E16:				$_{4}$FDGm		
E17:				$_{8}$FDGm		

CHAPTER 6: DISRUPTION OF SONG LEARNING BY IMPOSING A SPACE BETWEEN TUTOR AND TUTEE

6.1 Introduction

There are a variety of characteristics of tutor appearance and behaviour that have been shown to have a rôle in zebra finch song tutor selection. One shared feature is that they will all tend to increase tutee attention to a particular adult male. For example, this would be true of an aggressive tutor (Clayton 1987b), and in the cases where the amount and type of parental care has probably influenced tutor choice (Immelmann 1969, Eales 1987a, Clayton 1988, Williams 1990). Where learning has occurred preferentially from a bird of the parental morph (Chapter 2), from a paired male or from a male housed with the mother (Böhner 1983, Eales 1987b, Chapter 4 of this thesis), or from a male with a similar song to that of the father (Clayton 1987b), it can always be argued that these factors resulted in greater exposure to the chosen tutor.

Following from this, it is evident that learning from a particular tutor will become less likely where there is little opportunity for a close tutor-tutee association. At the extreme, this has been demonstrated by Eales (1989), who showed that zebra finches are reluctant to learn from adult males that can be heard but not seen, and will not learn at all where they can hear but not even vocally interact with a

tutor. Despite this finding, it is interesting that Adret (in prep.) has shown that learning from tape recordings is possible, but only provided that the young male has to key press for exposure to the song stimulus (thus introducing an interactive element).

In the more socially complex environment of an aviary (Chapter 5), the level of proximity between a tutee and an adult male was a good indicator of tutor selection, further suggesting that interactions occurring between closely associating birds may be important in song tutor choice. However, it is still unclear whether such close proximity is essential, if a tutor's song is to be successfully copied. Alternatively, this correlation found in the aviary may just be a reflection of the pattern described earlier, of a preference for learning from a bird with which there is increased exposure.

Can young male zebra finches learn a tutor's song if close proximity to the tutor is denied? An insight into this question comes from an experiment carried out by Patrice Adret (pers. comm.). In an attempt to control for variation in tutor behaviour (particularly song output), Patrice Adret set up a tutoring experiment in which he exposed several young zebra finches simultaneously to a single adult male. It was important that the juveniles could not see each other, while being housed at approximately the same distance from the tutor. The design incorporated a three-by-three matrix of small cages housing the young birds, with a single larger cage positioned 50cm away containing the tutor.

Despite the fact that the tutor sang frequently and that the tutoring period covered most of the acknowledged sensitive phase, none of the tutees (each of which had been female-raised) learnt the tutor's song. In fact, they developed highly abnormal song, more like that of birds raised in complete visual isolation from adult male zebra finches (Eales 1985b, 1987b).

Why this set-up did not lead to song learning is not clear. The distance separating the adult male from the juveniles was not great, and it would seem inconceivable that the tutees did not receive adequate auditory stimulation. Previous work had shown that the visual, as well as auditory, stimulation from a tutor can also be important in the song learning process (Eales 1989) but, again, the tutees' view of the adult male could not have been greatly impaired over just 50cm. It seems likely instead that the restricted interactions between tutor and tutees may have been the cause of the poor learning performance in the matrix cage.

To explore this possibility, Patrice Adret and I designed an experiment in which we could look further at the effect on song learning of imposing a gap between tutor and tutees. In particular, we were interested in closely monitoring the behaviour of young males, half of which were housed adjacent to the tutor's cage, while the rest were situated a short distance away. We predicted a superior learning performance by the "close" tutees but, in addition to this we were looking for behavioural correlations, within each group,

that might link with the amount of song copied. For example, "distant" tutees might be less attentive to the tutor, and thus exposed to him less. If so, do those birds that appear to pay him most attention learn better? Alternatively, levels of attention to the tutor may be equally high for all tutees, suggesting that other factors must cause the learning discrepancy - perhaps the tutor's responsiveness, for example.

6.2 Methods

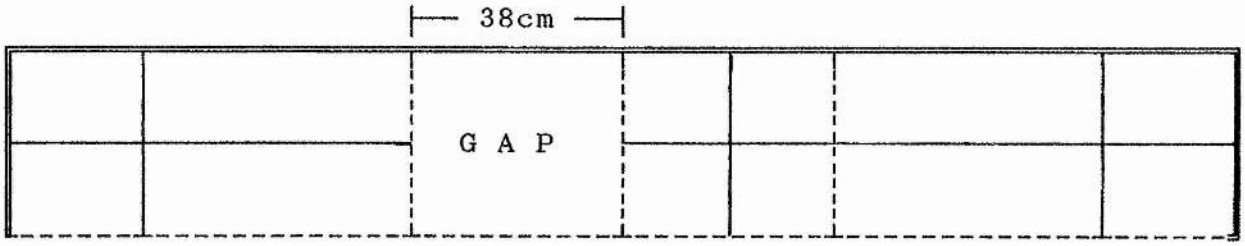
Experimental regime

The study involved six identical "triple" cages, each housing a tutor and two tutees (Figure 6.1). One of the latter was separated from the adult by only a mesh partition, while the other was separated by two partitions 38cm apart. The mesh used was made of fine wire and was of a relatively wide gauge (30x15mm); the reduced visibility through two partitions, as opposed to one, was considered to be negligible.

The 38cm gap separating the tutor and distant tutee was less than that in Adret's experiment (50cm). Although this might have resulted in a less severe block on song learning, we were more interested in the relative success achieved at the tutors' vocalisations, with the aim of correlating learning performance with behavioural data.

Figure 6.1 Plan of cage used in this experiment.

View from above.



Distant tutee Tutor Close tutee

——— Perch ---- Wire mesh partition/cage front

═══ Wooden sides and back to cage.

The tutee pairs were split into two groups of three. In Group 1, we used birds raised by the mother alone ("female-raised"), while in Group 2 both parents had previously been present ("normally-raised"). Two hypotheses were generated from this arrangement:

i) With female-raised birds, where there had been no exposure to zebra finch song prior to the experiment, we expected the close tutees to learn the song of the tutor quite accurately; in contrast, with the distant tutees we expected there to be a tendency towards the production of an abnormal song, with little evidence of learning (as occurred in Adret's original experiment, and as in some other studies, where female-raised birds received inadequate tutoring through the sensitive phase [e.g. Eales 1985b]).

ii) With normally-raised birds we predicted that fully developed song phrases would occur in both close and distant tutees; however, in this case we expected a tendency towards the latter group producing at least some elements of their fathers' songs. This effect has been found in previous studies, where normally-raised birds were exposed to inadequate tutoring after independence (Eales 1985b, Böhner 1986, Clayton 1987c, 1988, Chapter 2 of this thesis).

Two male siblings, reared together, formed each pair of tutees, to minimise differences in early, pre-tutoring experience which might have an effect on the results. This was especially important in the case of the normally-raised birds, where exposure to different songs prior to

independence might have altered the likelihood of the tutor's song being copied.

The young male finches were housed with their parents, or just their mother, until day 35, when they were moved into the experimental cages. They remained in the tutoring set-up until day 65, after which they were kept in individual isolation (in sound-proof boxes) until their songs had been recorded (between days 100 and 120). In the tutoring phase, birds were kept in other cages within the same room, but none of these could be seen at a distance of closer than approximately 3m.

Song analysis

This experiment involved comparing the learning performance of two birds. To allow this, it was important to be able to quantify the amount of learning and to make it as objective as possible. A problem here was that some birds developed quite crude songs, and simply counting the elements copied from the tutor ignores differences that exist in aspects such as copying accuracy and syntax. It was decided, therefore, that the song analysis should be approached from more than one direction.

1. At the first level, the number of elements copied from the tutor (or father) was established, by comparing sonagrams by eye. These data show where learning has clearly taken place; also, where there is a large discrepancy in the number of elements apparently incorporated from the tutor's

song, between the two tutees, a confident claim can be made about the difference in learning performance. However, where the difference in the number of copied elements is slight, we have to be more careful. The precise method of splitting and numbering elements during the analysis can alter the scoring, and it is also possible that certain elements are intrinsically more difficult to copy than others. In fact, there is probably no completely satisfactory definition for an element; it was decided, therefore, to score the amount of copying from the adults by using a combination of two methods (see Appendix 6.1, for definitions and further discussion of the problem). This was done by taking the mean of the two percentage values obtained.

2 . In addition to looking at whether elements have been copied from a tutor it is also relevant to look at syntax. After a juvenile zebra finch male has acquired a complement of elements in its repertoire, there follows an organisational stage involving a transition from more-or-less randomly produced strings of elements to discrete, repeated phrases with fixed element sequence (Immelmann 1969). In previous studies where birds have been reared in conditions not conducive to song learning, normal adult syntax has often not been achieved. Therefore, in this experiment, we might expect a greater degree of stereotypy from the close tutees than from the distant tutees. The

fixity of syntax, termed "phrase consistency", was measured as follows:

$$\frac{\text{number of phrases with most common sequence of elements} + \text{number of phrases with } 2^{nd} \text{ most common sequence}}{\text{total number of phrases sampled}} \times 100$$

The second most common phrase-types were included in the numerator, because a regular feature of many normal zebra finch songs is the occurrence of a slightly different phrase at the start or end of a bout (sometimes an element or two is missing from the first phrase, or additional elements may be added to later phrases).

This criterion was measured for the tutors, as well as tutees, so that the levels of phrase consistency expected in normally singing adults would be known.

3. Finally, various other unusual features of the tutee songs were noted. These included repeats of the same element, and elements with an abnormal, or particularly variable, structure.

Other aspects of song that could have been measured were considered for analysis, but rejected as unsuitable (see Appendix 6.2). These included measurements of phrase length, pause length (between phrases) and tempo (number of elements/second within a phrase).

BEHAVIOURAL OBSERVATIONS

Throughout the 30 days of exposure to the song tutor, behavioural observations of the experimental birds were made from behind a "hide" (at least 11 watches per cage; see Figure 6.2). Each observation period lasted one hour, and was split as follows:

a) 20 minutes collecting data on the positions of the three birds in their respective cages. This was done by means of "instantaneous sampling", every 30 seconds. Bird locations were marked onto tracing paper overlays, positioned above a scale plan of the cage. Also during this 20 minute period, we recorded the amount of time spent feeding, preening, resting/sleeping and singing (again by on-the-dot sampling at 30 second intervals).

Then either:

b) 40 minutes collecting data on behaviour associated particularly with occurrences of bouts of tutor song. A "bout" here is defined as a series of song phrases separated from the previous series by at least 10 seconds. The positions of the tutees were mapped as accurately as possible onto cage plans, as soon as the tutor started to sing. What they were doing at that time was recorded (feeding, preening, singing, resting or "other"), as was their immediate reaction following the start of the song bout (approach or move away from the singing male, or remain as before). New data were collected every time the tutor started a fresh song bout. Where possible, data were

Figure 6.2 Spread of observations on the six cages, with respect to tutee age.

Tutee age (days)	Cage number					
	1a	1b	2	3	4	5
35	X	X				
36	X	X	X			
37	X	X	X	X		
38				X	X	X
39	X		X		X	
40				X	X	
41		X	X	X		X
42			X	X		X
43			X		X	
44	X	X				
45			X			
46			X	X		X
47					X	
48	X	X				
49			X			X
50	X	X	X		X	
51	X	X				
52	X		X			X
53				X	X	
54	X	X		X		
55			X			X
56	X	X	X		X	X
58	X	X		X		X
59	X	X	X			X
60	X				X	
61	X			X		
62	X			X		X
63	X	XX	X		X	X
64		X				X
65				X		
66			X			

X - denotes a single observation on a cage. Most lasted for one hour, and followed the procedure described in the Methods. The only exceptions were the earliest four watches on cage 1a, which were organised slightly differently and were therefore excluded from most of the analyses.

collected separately for "directed" and "undirected" song bouts (this often proved to be quite difficult, as will be discussed).

or:

c) 40 minutes collecting data on the position and body orientation of the singing tutor (directed or undirected song). Again, this was done at the start of every song bout, but also, where possible, when changes in orientation occurred during a bout. These data enabled us to find out which tutee the tutor tended to face when singing: having more song directed towards it might lead to an individual learning more accurately.

During the 40 minute section, of either type, data were also collected on the subsong output of the juveniles (scored by one-zero sampling in each minute), and on relative levels of activity of all experimental birds. For the latter, birds were watched for five one-minute periods, each at least three minutes apart, within which the number of changes of perch position were scored. Zebra finches tend to move by distinct hops or flights, so scoring events was usually straightforward. When birds were on the floor of the cage, however, movements were less clear-cut; it was decided to stop counting completely during feeding bouts, and otherwise to score only when more than three bird-lengths had been moved.

This behavioural measure was taken because when a tutor, for example, is particularly active, it may increase

attentiveness towards him and song learning may be more likely to occur. Also, it was possible that the amount of activity of the close tutees would differ from that of the distant tutees, perhaps because of a greater tendency to approach the tutor.

In all cases above where positions of birds were being recorded, the data were later digitised from the scale drawings with a program written in Turbo Pascal 4.0 and run on a Zenith 159-13 Personal Computer. The program was written such that plots of bird positions could be made directly from the stored data.

6.3 Results

SONG ANALYSIS

Table 6.1 shows the amount of song that the juveniles copied from the tutor and also from the father, in the case of the normally raised birds. Table 6.2 lists the phrase consistency values calculated for the tutees and includes comments on any abnormal song features that were found.

All but one of the close tutees learnt more of the tutors' songs than did distant tutees. This is just significant (Table 6.3). Female-raised birds that produced fewer of their tutor's elements, tended to fill their own songs with more improvised notes (Table 6.4), but the correlation did not quite reach significance. Normally raised birds that

Table 6.1 Source of song of the tutees.

Female-raised birds:

CAGE N°.	TUTEES	T	% of song of T copied	% of elements unassigned
1b	J360C	T249	73.9	19.5
1b	J359D	T249	37.0	61.8
2	J389C	T506	76.4	18.6
2	J390D	T506	76.4	13.4
5	J367C	T119	73.9	45.7
5	J368D	T119	41.5	39.6

Normally raised birds:

CAGE N°.	TUTEES	F	T	% of song of F copied	% of song of T copied	% of elements unassigned
1a	J212C	F165	T29	46.5	61.3	9.7
1a	J211D	F165	T29	84.5	38.8	39.1
3	J115C	F78	T162	0.0	80.6	0.0
3	J113D	F78	T162	71.4	13.9	12.5
4	J161C	F60	T224	31.7	81.7	22.5
4	J135D	F60	T224	58.1	27.5	0.0

F - father T - tutor J - juvenile

Each bird is identified by its status code (F, T or J) followed by its ring number and then, if a juvenile, by C (close tutee) or D (distant tutee).

The percentages in the table were calculated by taking the mean of the values obtained using the two element definitions (see Appendix 6.1).

Table 6.2 Phrase consistency and unusual features of the tutee songs.

CAGE NO.	TUTEES	PHRASE CONSISTENCY %	UNUSUAL FEATURES OF SONG
FEMALE-RAISED BIRDS			
1b	J360C	100.0	Introductory notes are loud, like call notes
1b	J359D	78.6	Element C is sometimes of unusually long duration. Some plasticity still in song.
2	J389C	100.0	-
2	J390D	100.0	(Perhaps less clearly defined elements than in J390C).
5	J367C	81.3	-
5	J368D	100.0	Element D is of unusually high frequency. Song sounded slurred.
NORMALLY RAISED BIRDS			
1a	J212C	100.0	-
1a	J211D	30.4	Very little stereotypy. Also elements variable, especially Element E (resembles note from birds reared in isolation).
3	J115C	92.5	-
3	J113D	73.3	Element F repeated within the phrase.
4	J161C	91.2	-
4	J135D	40.3	Element order varies much more than "phrase consistency indicates (21-plus different combinations). The element group G is quite variable in form. Element H is of unusually long duration.

Phrase consistency is defined in the Methods.

The specific elements referred to in the table are labelled in Appendix 6.3.

Table 6.3 Comparison of the amount of copying from the tutor by the close and distant tutees.

	Elements copied from tutor:	
Cage number	Close tutees	Distant tutees
1b	6.75	4.00
2	6.50	6.50
5	7.00	3.50
1a	4.00	2.50
3	6.00	1.00
4	4.50	2.00

Wilcoxon matched pairs test, n for test = 5, W = 15, one-tailed, p = 0.03.

Note - the "number of elements copied" was calculated by taking the mean of the scores obtained using the two element definitions.

With definition A, there were occasions when only part of a particular tutor element was copied. Where this was the case a copying score of 1/2 or 1/3 was used, depending on how many component elements the tutor element consisted of, in terms of definition B. Hence, in this table (and also in Table 6.8) the number of elements copied is not always the average of two whole numbers.

Table 6.4 The relationship in female-raised birds between the amount of song copied from the tutor, and the proportion of improvised elements.

% of tutor's song copied	% of improvised elements
76.4	18.6
76.4	13.4
73.9	19.5
73.9	45.7
41.5	39.6
37.0	61.8

Pearson correlation coefficient (after arcsine transformation): $r = -0.767$, $df = 4$.

Critical value = 0.811, therefore NS.

Note - it was not inevitable that a significant, or near-significant result would be obtained here. Birds copying less from the tutor could simply produce shorter songs.

copied little from the tutor seemed to be compensating by copying more from the father, but again the result was not quite significant (Table 6.5). In cases where the tutoring was inadequate, the latter group also increased the number of elements in their songs by improvisation. However, in these situations, there was more of a tendency, that approached significance, to recall elements from the father's song (Table 6.6). On average, the female-raised birds tended to have a higher percentage of improvised elements in their songs than those normally-raised (Table 6.7).

The consistent pattern in these initial analyses, of correlations approaching but not quite achieving significance, suggests that real effects were probably involved, but were obscured because of the small sample of birds in the experiment. Consequently many of the comments about these, and later, results must necessarily be of a tentative nature.

At an anecdotal level, within the normally-raised birds, the distant tutees produced more from their fathers' songs than did the close tutees. In fact, in all three of the relevant cages, the close tutees produced more elements from the tutor than from the father, while the opposite was true for the distant tutees.

The "phrase consistency" (pc) of the adult males (fathers and tutors) involved in this experiment varied between 70.8% and 100% (mean = 89.4, sd = 9.76; Table 6.8). Close tutees

Table 6.5 The relationship in normally-raised birds between the amount of song copied from the tutor, and the amount copied from the father.

% of tutor's song copied	% of father's song copied
81.7	31.7
80.6	0.0
61.3	46.5
38.8	84.5
27.5	58.1
13.9	71.4

Pearson correlation coefficient (after arcsine transformation): $r = -0.796$, $df = 4$.

Critical value = 0.811, therefore NS.

Table 6.6 Improvising versus recalling elements learnt from the father, as a way of supplementing the song in normally-raised birds.

Number of elements copied from father	Number of elements improvised
2.75	0.75
6.75	6.25
0.00	0.00
6.00	1.00
2.50	2.00
5.88	4.00

Wilcoxon matched pairs test, n for test = 5, two-tailed, W = 15, p = 0.059.

Table 6.7 Did female-raised birds tend to improvise song elements more so than do normally-raised birds?

Number of improvised elements:

Female-raised birds	Normally-raised birds
6.50	6.25
5.67	2.00
2.75	1.00
1.75	0.75
1.00	0.00
1.00	0.00

Mann-Whitney U Test, n = 6, m = 6, U = 30:
p = 0.09, not significant.

Table 6.8 The "phrase consistency" of the adult males used in the experiment.

Tutor	n	N1	N2	Phrase consistency
T249	32	19	9	87.5
T119	18	11	6	88.9
F165	24	22	1	95.8
T29	24	23	1	100.0
F78	24	9	8	70.8
T162	30	14	13	90.0
F60	34	22	6	82.3
T224	11	8	3	100.0

Phrase consistency = [(N1+N2)/n] x 100

where,
n - sample of phrases analysed.
N1 - frequency of phrases with commonest element sequence.
N2 - frequency of phrases with second most common element sequence.

The tutor T506 is not included in the table because too few of his song phrases had been recorded to allow a reliable estimate to be made of its phrase consistency.

did not quite show a higher pc value than distant tutees (Table 6.9). However, the small sample size is likely to have been responsible for this result, because there was a significant positive correlation between the amount of learning from the tutor and the measure of phrase consistency (Table 6.10). The pc values of all the close tutees fell within the adult range, while two of the distant tutees had an abnormally low pc (30.4% and 40.3%). Interestingly, the tutee that copied the least from the tutor was not one of these birds.

BEHAVIOURAL DATA

The mean tutor-tutee distance differed significantly between the five close tutees and the five distant ones (Figure 6.3). Within each group, in all but one case where there was a significant difference in tutor-tutee proximity, the close tutee had learnt more from the tutor (13 out of 14, Table 6.11). Even so, this was not sufficient to give a significant negative correlation between the amount of tutor song copied and the mean distance apart, for either close or distant tutees (Table 6.12).

Mean tutor-tutee proximity may be a less relevant measure than the proportion of time that the birds spend within certain distances of each other. For example, accurate song learning may be strongly facilitated by interactions taking place at very close range. It is possible that two birds can have the same proximity mean, even though only one of them has spent much time within this critical distance.

Table 6.9 Comparison of the phrase consistency of close and distant tutees.

	Close tutees			Distant tutees		
Cage	n	N1+N2	pc (%)	n	N1+N2	pc (%)
1a	6	6	100.0	23	7	30.4
1b	42	42	100.0	14	11	78.6
2	35	35	100.0	38	38	100.0
3	53	49	92.5	15	11	73.3
4	34	31	91.2	57	23	40.3
5	16	13	81.3	20	20	100.0

Wilcoxon's matched pairs test, one-tailed, W = 14, n for test = 5, p = 0.053.

pc - phrase consistency.
n - sample of phrases analysed.
N1 - frequency of phrases with commonest element sequence.
N2 - frequency of phrases with second most common element sequence.

Table 6.10 Correlation of phrase consistency with the amount of song copied from the tutor.

Tutee	Phrase consistency (%)	% of tutors song copied
J360	100.0	73.9
J389	100.0	76.4
J390	100.0	76.4
J368	100.0	41.5
J212	100.0	61.3
J115	92.5	80.6
J161	91.2	81.7
J367	81.3	73.9
J359	78.6	37.0
J113	73.3	13.9
J135	40.3	27.5
J211	30.4	38.8

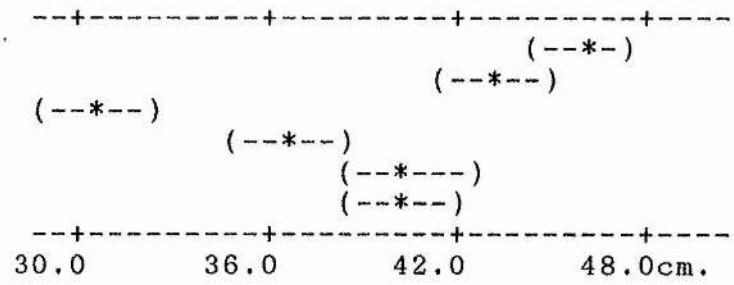
Pearson correlation coefficient (after arcsine transformation): $r = 0.588$, $df = 10$.

Critical value = 0.576, therefore SIGNIFICANT.

Figure 6.3 Proximities of close and distant tutees to the tutor, throughout the sensitive phase.

Close tutees

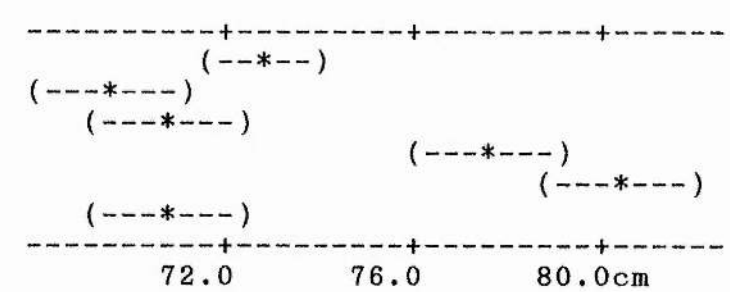
Cage	N	MEAN	STDEV
1a	780	46.17	20.48
1b	632	43.22	23.67
2	561	30.78	17.66
3	559	36.75	20.46
4	431	40.41	22.89
5	504	40.00	20.56



Analysis of variance, degree of freedom = 5, F = 40.78: $p < 0.001$, significant.

Distant tutees

Cage	N	MEAN	STDEV
1a	780	72.83	21.21
1b	632	69.55	19.11
2	561	70.66	15.92
3	559	77.76	20.04
4	431	80.41	20.95
5	504	70.72	14.06



Analysis of variance, degree of freedom = 5, F = 27.61: $p < 0.001$, significant.

The proximity measure is the mean distance between a tutor and tutee, with data combined from all watches.

n is the number of instantaneous samples in which tutor-tutee distance was measured.

Shown in the figure are these mean distances, with 95% confidence intervals based on the pooled standard deviation.

Table 6.11 In paired comparisons, did the tutees that had a significantly lower mean proximity to the tutor learn better?

	Nearest (n)	Furthest (f)	P value(*)	Tutee that copied most from tutor
CLOSE TUTEES				
	J389	J212	0.0001	J389 - n
	J389	J360	0.0004	J389 - n
	J389	J161	0.0320	J161 - f
	J389	J367	?	J389 - n
	J115	J212	0.0083	J115 - n
	J115	J360	0.0350	J115 - n
DISTANT TUTEES				
	J211	J135	0.0330	J211 - n
	J211	J113	0.0140	J211 - n
	J359	J135	0.0035	J359 - n
	J359	J113	0.0001	J359 - n
	J390	J135	0.0190	J390 - n
	J390	J113	0.0045	J390 - n
	J368	J135	0.0084	J368 - n
	J368	J113	<0.0001	J368 - n

* - P VALUE calculated from paired t-tests, using data from all observations.

Excluded from the table were the pairs, within both close and distant groups, that did not differ in their mean proximities to the tutor.

A statistical analysis of the above pattern, testing whether birds spending more time near to their tutor tended to copy more of his song, is not possible because of a problem of non-independence. Nevertheless, there is strong hint of a genuine effect.

Table 6.12 Correlation between the mean proximity to the tutor and the amount of song copied from him.

Cage	CLOSE TUTEES Proximity (mean)	% of song copied	DISTANT TUTEES Proximity (mean)	% of song copied
1a	45.2	61.3	72.9	38.8
1b	43.3	73.9	69.6	37.0
2	30.7	76.4	70.6	76.4
3	36.6	80.6	77.9	13.9
4	40.5	81.7	80.4	27.5
5	40.2	73.9	70.8	41.5

Close tutees:

Pearson correlation coefficient (after arcsine transformation): $r = -0.537$, $df = 4$.

Critical value = 0.811, therefore NS.

Distant tutees:

Pearson correlation coefficient (after arcsine transformation): $r = -0.648$, $df = 4$.

Critical value = 0.811, therefore NS.

The "proximity" in the table is the measure of that between the tutor and tutee through all of the observations.

However, the proportion of time that the tutor and close tutee spent within 12cm, or 24cm, of each other, also did not correlate significantly with the amount of the tutor's song that had been learnt, but the correlation coefficients were nevertheless quite high (0.64 and 0.77 respectively, Table 6.13). There was no such hint of a correlation in the case of the distant tutees and distances of less than 50cm or less than 62cm. For both sets of tutees, the correlation was better using the larger distance, and it is perhaps interesting that the two distant tutees and three close tutees that copied least from the tutor also spent the least time near to him.

Certain patterns are apparent from the plots of bird positions in each cage. For example, the distant tutee in cages 5 and 2 spent proportionally more of their time right by the partition, than did the distant tutees in the other cages (Figure 6.4). These also happen to be the two distant tutees that learnt the most from the tutor. That they were not also within closest proximity to the tutor, based on the data from Table 6.12, implies that the tutor in these cases must have been spending much of his time at the far side of his cage.

Correlating the amount of time spent in the 25% of the cage nearest the tutor, with song learning performance again gives insignificant results, for both sets of tutees (Table 6.13). Also, there was no evidence of a relationship between the time spent by the tutor near to a tutee's cage, and the amount of its song that was learnt (Table 6.15).

Table 6.13 Correlations between the amount of time spent within certain proximities of the tutor, and the amount of song copied.

CLOSE TUTEES

a) Cage	% of time within 12cm of tutor	% of time within 24cm of tutor	% of tutor's song copied
1a	4.5	7.2	61.3
1b	10.0	16.0	73.9
2	19.1	33.9	76.4
3	8.9	24.9	80.6
4	13.2	21.6	81.7
5	11.9	21.4	73.9

< 12cm: Pearson correlation coefficient (after arcsine transformation): r = 0.636, df = 4.

Critical value = 0.811, therefore NS.

< 24cm Pearson correlation coefficient (after arcsine transformation): r = 0.770, df = 4.

Critical value = 0.811, therefore NS.

DISTANT TUTEES

a) Cage	% of time within 50cm of tutor	% of time within 62cm of tutor	% of tutor's song copied
1a	11.4	44.9	38.8
1b	16.1	45.9	37.0
2	6.6	34.4	76.4
3	5.9	27.2	13.9
4	5.3	23.7	27.5
5	3.0	31.3	41.5

< 50cm: Pearson correlation coefficient (after arcsine transformation): r = 0.026, df = 4.

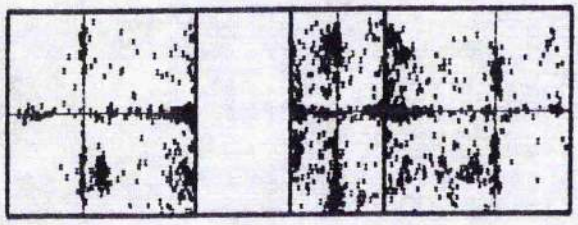
Critical value = 0.811, therefore NS.

< 62cm: Pearson correlation coefficient (after arcsine transformation): r = 0.312, df = 4.

Critical value = 0.811, therefore NS.

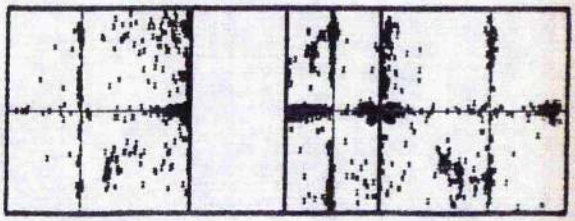
Figure 6.4 Plots of bird positions throughout all observations.

CAGE 1a



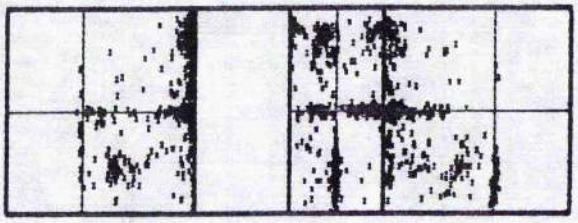
BIRD: J211 T29 J212

CAGE 1b



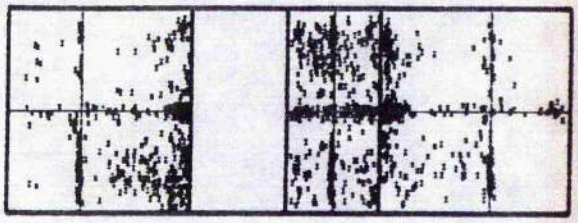
J359 T249 J360

CAGE 2



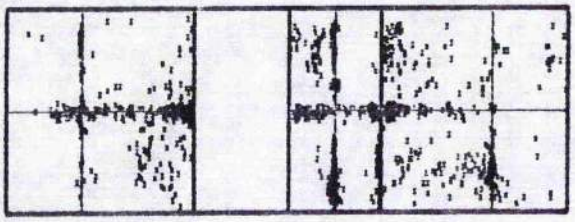
BIRD: J390 T506 J389

CAGE 3



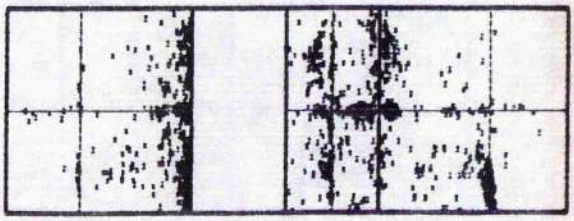
J113 T162 J115

CAGE 4



BIRD: J135 T224 J161

CAGE 5



J368 T119 J367

J - Juvenile T - Tutor.

The black marks in each cage represent the positions of the tutors and tutees recorded by instantaneous sampling, every 30 seconds, through all focal watches.

The narrow lines within each cage are perches

Table 6.14 Correlations between the amount of time spent within close proximity of the partitions, and he amount of song copied.

CLOSE TUTEES

Cage	n(*)	% of time spent within 19cm (+) of partition	% of tutor's song copied
1a	780	60.4	61.3
1b	632	60.8	73.9
2	561	81.1	76.4
3	559	75.5	80.6
4	423	64.3	81.7
5	504	54.0	73.9

Pearson correlation coefficient (after arcsine transformation): r = 0.420, df = 4.

Critical value = 0.811, therefore NS.

DISTANT TUTEES

Cage	n(*)	% of time spent within 19cm (+) of partition	% of tutor's song copied
1a	780	68.7	38.8
1b	632	76.6	37.0
2	561	80.9	76.4
3	559	64.6	13.9
4	423	56.5	27.5
5	504	88.9	41.4

Pearson correlation coefficient (after arcsine transformation): r = 0.577, df = 4.

Critical value = 0.811, therefore NS.

* - number of instantaneous samples form which data extracted.

+ - 19cm was selected simply because it is a quarter of the cage length.

Table 6.15 Correlations between the amount of time spent by the tutor within close proximity of the left and right partitions, and the amount of song copied by the two tutees.

Cage	n(*)	% of time spent by tutor within 13cm(+) of partition nearest close tutee	% of tutor's song copied by close tutee
1a	780	15.0	61.3
1b	632	23.7	73.9
2	561	38.3	76.4
3	559	29.2	80.6
4	423	27.2	81.7
5	504	42.3	73.9

Pearson correlation coefficient $r = 0.513$, $t = 1.195$, $df = 4$, $p > 0.20$, not significant.

Cage	n(*)	% of time spent by tutor within 13cm(+) of partition nearest distant tutee	% of tutor's song copied by distant tutee
1a	780	30.0	38.8
1b	632	32.3	37.0
2	561	18.0	76.4
3	559	24.3	13.9
4	423	21.7	27.5
5	504	11.9	41.4

Pearson correlation coefficient $r = -0.320$, $t = 0.67$, $df = 4$, $p > 0.20$, not significant.

* - number of instantaneous samples from which data extracted.

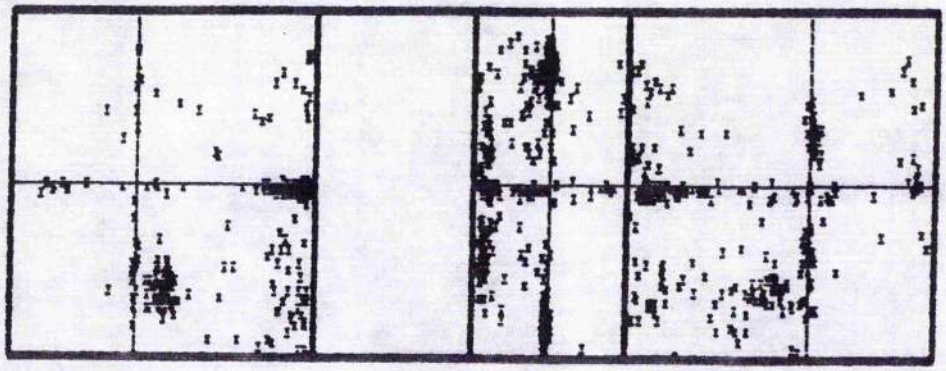
+ - 13cm was selected because this is approximately a third of the length of the tutor's cage.

The lack of strong correlations between proximity and learning performance could conceal genuine underlying effects, if this criterion is important but at a restricted time within the 30 day period, when the tutees are more susceptible to the stimulus provided by the singing tutor. The data were split such that proximity measures could be obtained for each of three parts of the sensitive phase, 35 to 44 days (A), 45 to 54 days (B) and 55 to 66 days (C) (see Figures 6.5 a-f). Within all three periods for each group of tutees, close and distant, there were highly significant differences between cages in tutor-tutee proximity (Figure 6.6). However, there was no consistent trend in the pattern of proximity over the 30 days, with eight birds showing an increased mean distance to the tutor between period A and C, while four birds showed a decrease. Correlations with song learning over the three periods produced the strongest negative relationships between 35 and 44 days for distant and close tutees, with the value very nearly reaching significance for the latter group (Table 6.16). It is curious, but perhaps insignificant, that particularly low correlations (approaching zero) occurred in period B. All six correlations turned out to be in the same direction. This indicates that there may be a tendency to learn more successfully with an increased tutor proximity, even within the close and distant groups, but the effect is slight, probably owing to the involvement of other behavioural factors (and because the sample size is small).

In period A, J212 from cage 1a tended to be considerably further from the tutor than the other close tutees

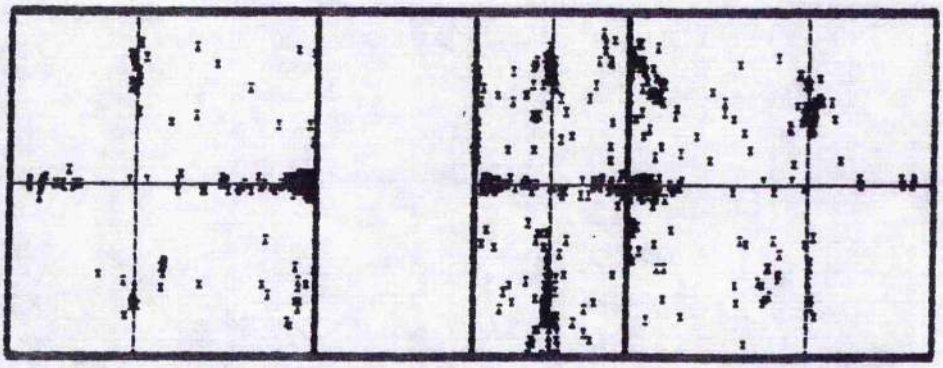
FIGURE 6·5a Locations of the tutor and tutees in three parts of the sensitive phase.

CAGE 1A

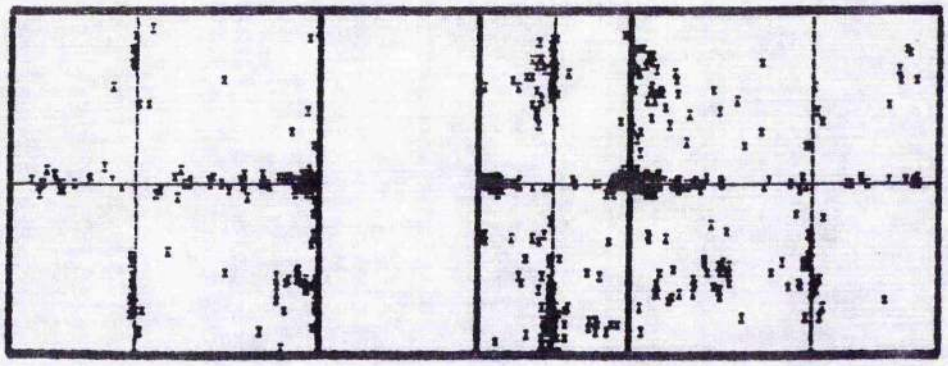


A. 35-44 days.

BIRD: J211 T29 J212



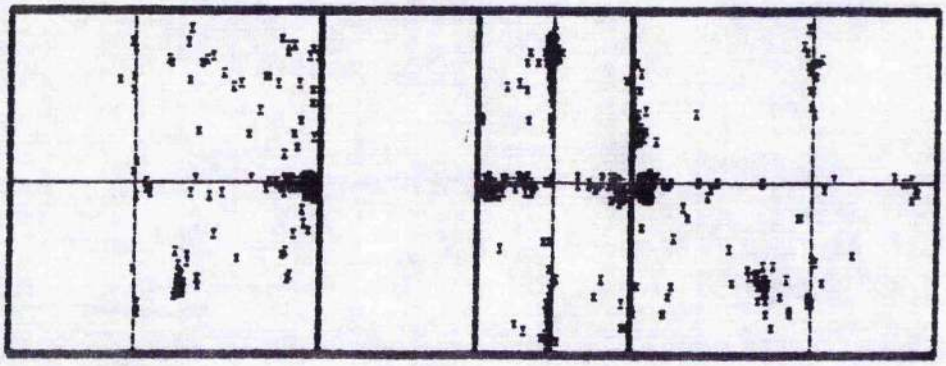
B. 45-54 days.



C. 55-66 days.

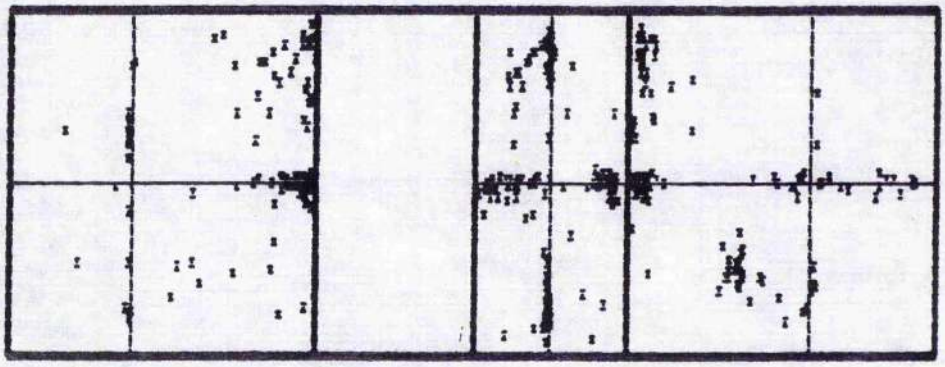
FIGURE 6·5b

CAGE 1B

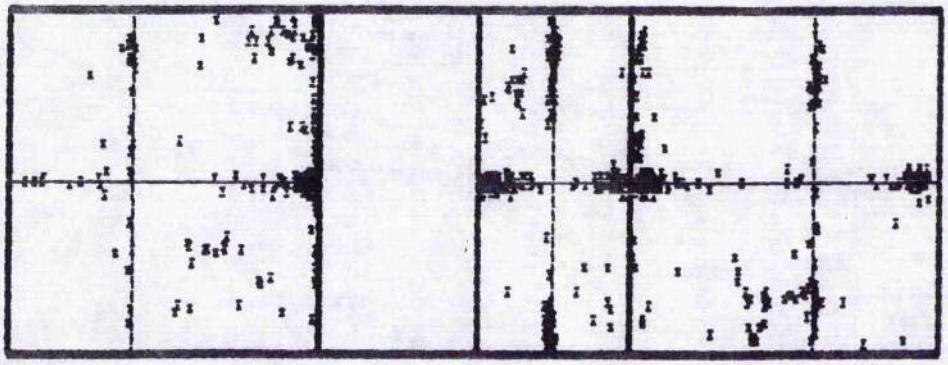


A. 35-44 days.

BIRD: J359 T249 J360



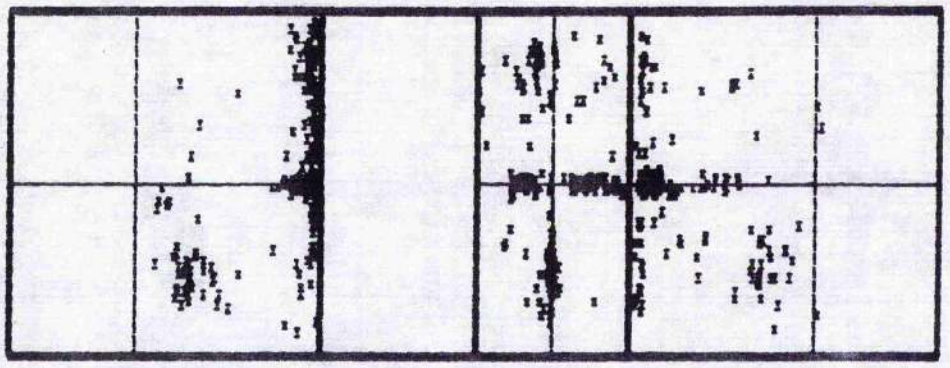
B. 45-54 days.



C. 55-66 days.

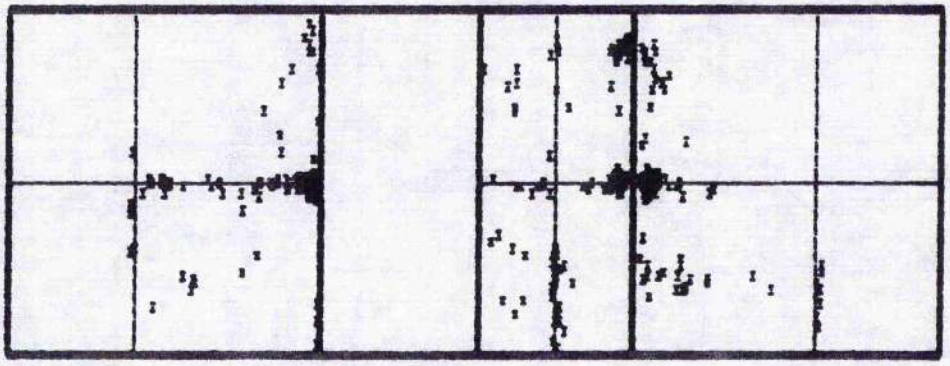
FIGURE 6.5c

CAGE 2

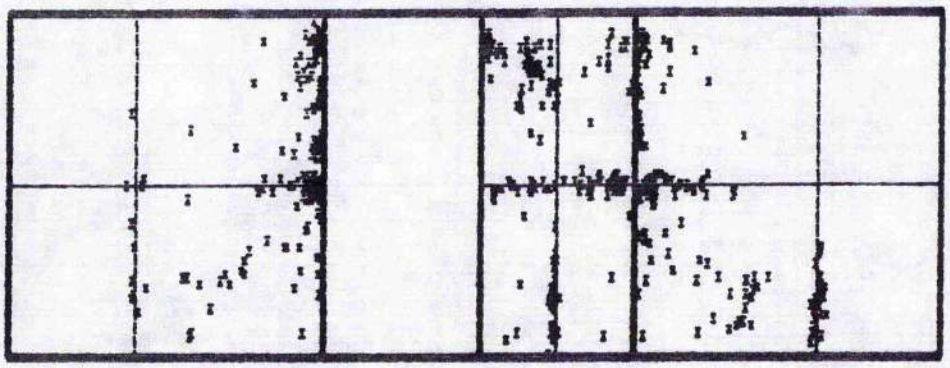


A. 35-44 days.

BIRD: J390 T506 J389



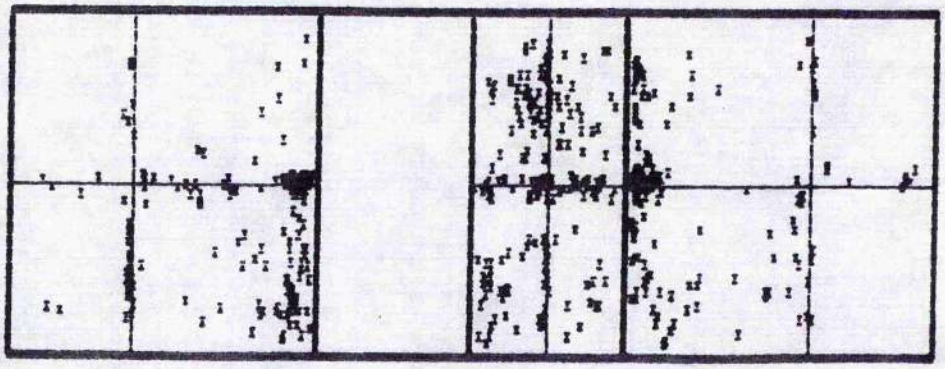
B. 45-54 days.



C. 55-66 days.

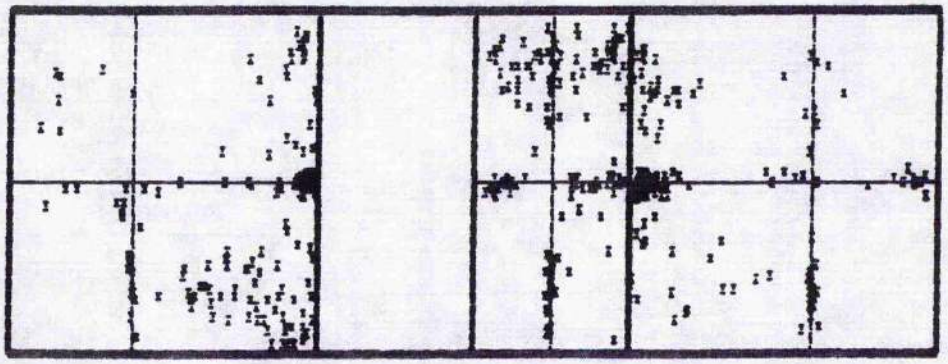
FIGURE 6.5d

CAGE 3

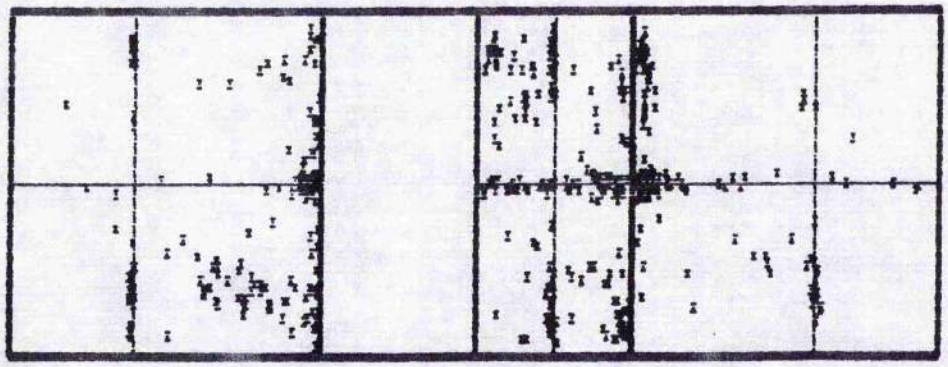


A. 35-44 days.

BIRD: J113 T162 J115



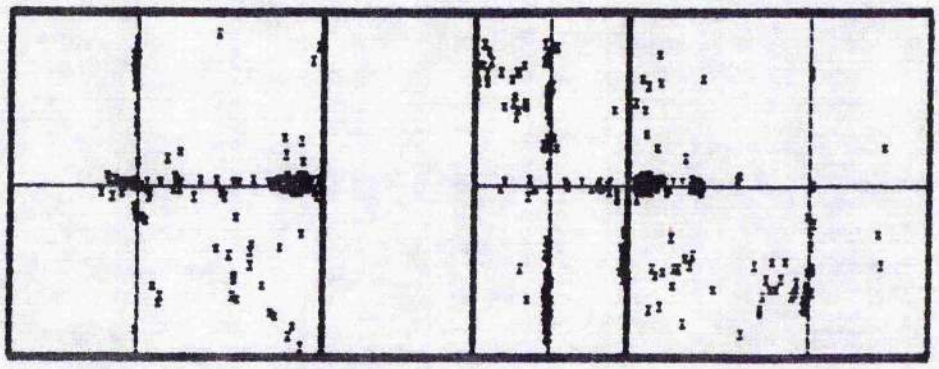
B. 45-54 days.



C. 55-66 days.

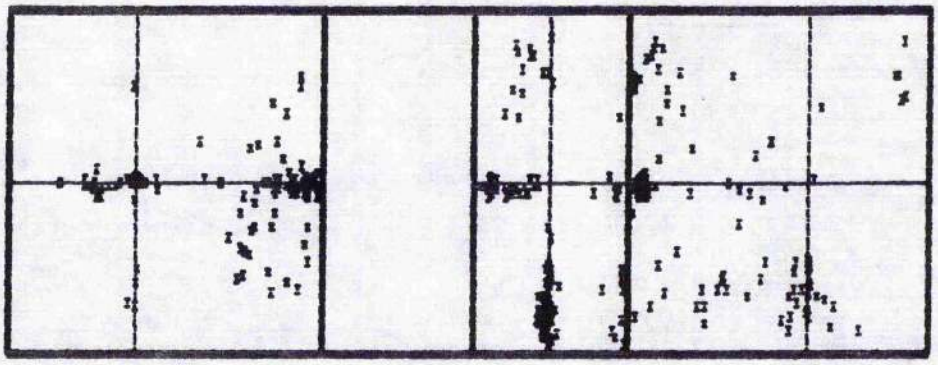
FIGURE 6.5e

CAGE 4

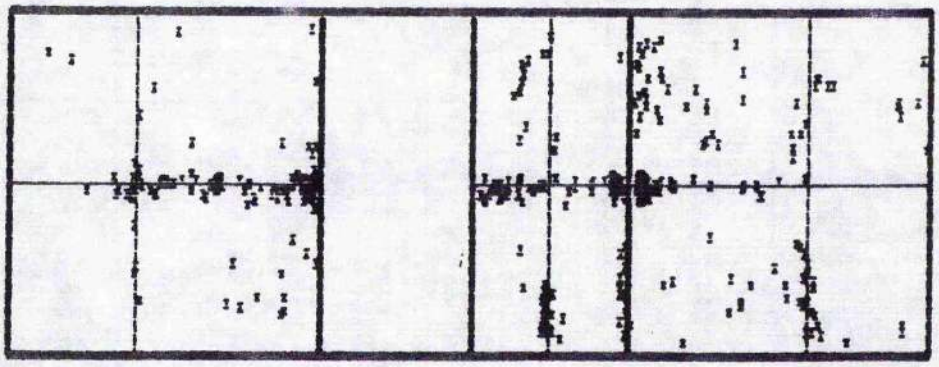


A. 35-44 days.

BIRD: J135 T224 J161



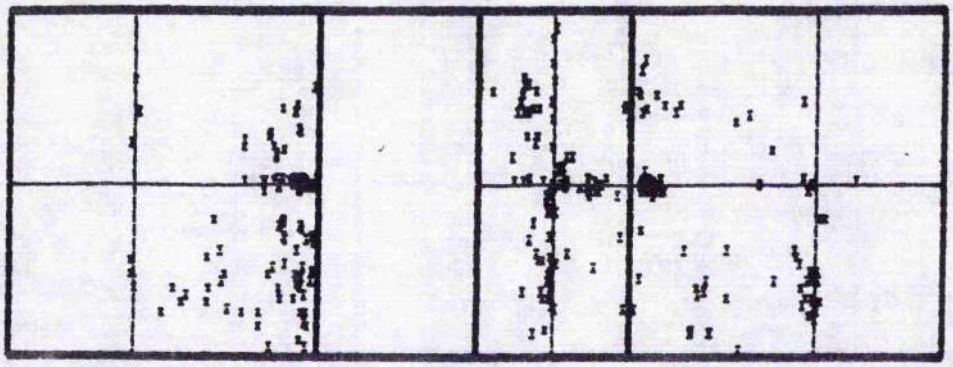
B. 45-54 days.



C. 55-66 days.

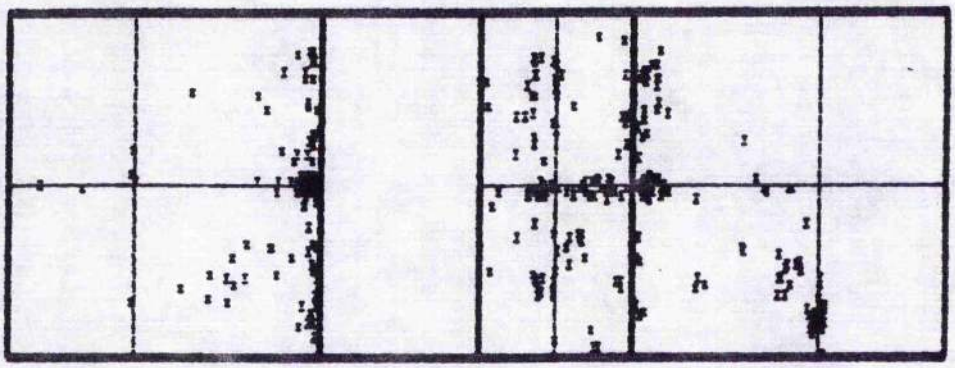
FIGURE 6.5f

CAGE 5

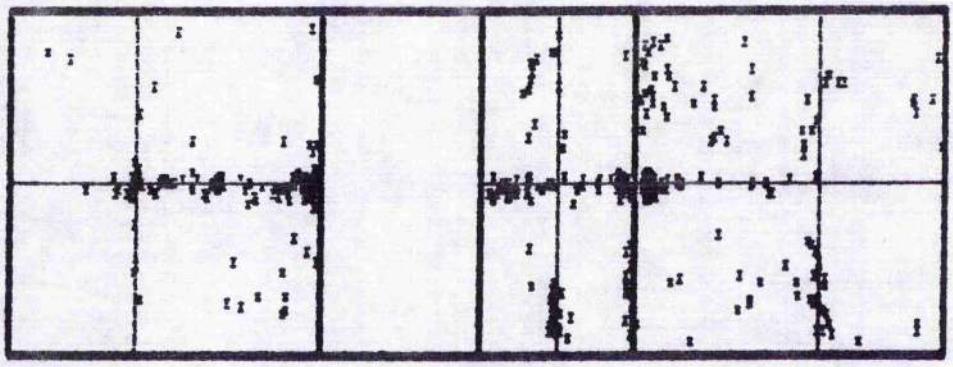


A. 35-44 days.

BIRD: J368 T119 J367



B. 45-54 days.



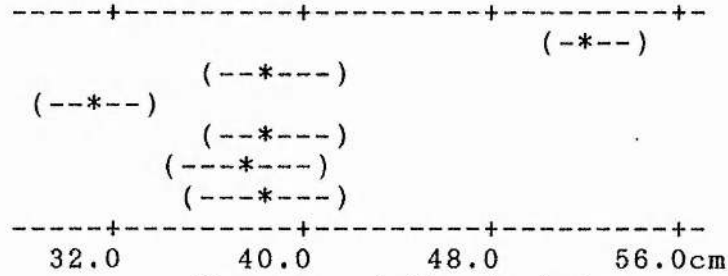
C. 55-66 days.

Figure 6.6 Variation in tutor-tutee proximity over three periods of the sensitive phase.

CLOSE TUTEES

PERIOD A: 35-44 DAYS

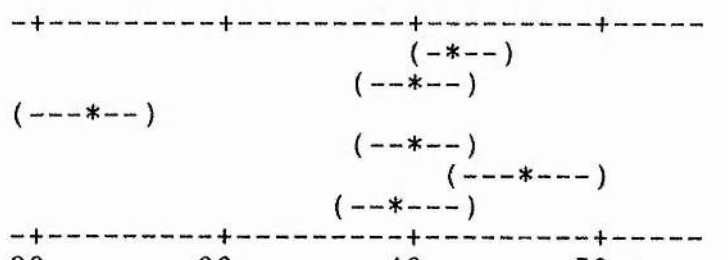
Cage	N	MEAN	STDEV
1a	296	52.28	20.44
1b	202	38.68	21.93
2	237	31.00	15.06
3	200	38.55	19.23
4	160	37.72	19.51
5	115	38.47	16.99



Mean proximity to tutor
(with 95% confidence intervals based on pooled standard deviation)

PERIOD B: 45-54 DAYS

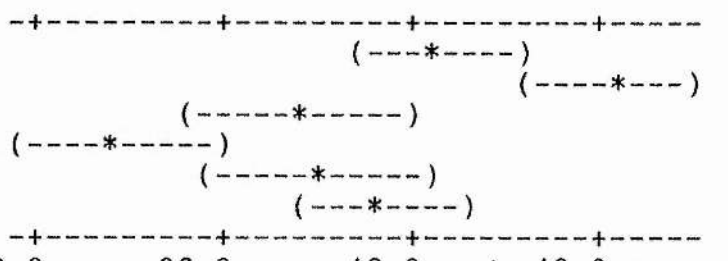
Cage	N	MEAN	STDEV
1a	243	42.11	19.35
1b	159	40.00	20.28
2	161	22.50	17.30
3	160	39.63	23.04
4	119	45.96	20.92
5	120	39.33	18.73



Mean proximity to tutor

PERIOD C: 55-66 DAYS

Cage	N	MEAN	STDEV
1a	241	42.76	19.90
1b	271	48.49	25.71
2	165	38.44	17.91
3	199	32.64	18.83
4	152	38.89	26.74
5	269	40.95	22.64



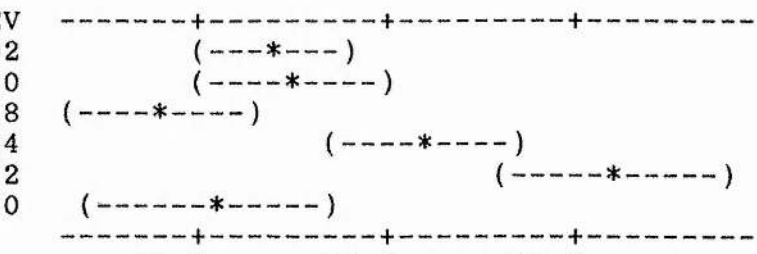
Mean proximity to tutor

Figure 6.6 (continued)

DISTANT TUTEES

PERIOD A: 35-44 DAYS

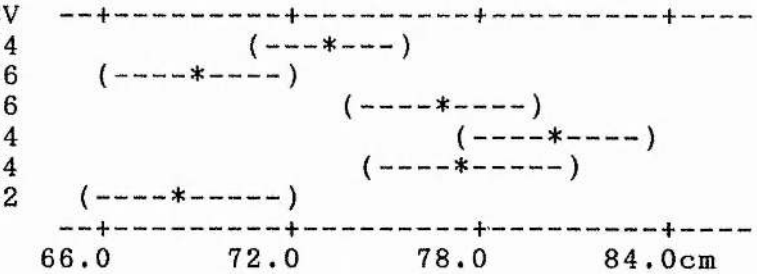
Cage	N	MEAN	STDEV
1a	296	72.00	20.02
1b	202	72.70	19.00
2	237	68.95	13.48
3	200	76.06	19.34
4	160	80.97	20.12
5	115	70.39	13.70



Mean proximity to tutor
(with 95% confidence intervals based on pooled standard deviation)

PERIOD B: 45-54 DAYS

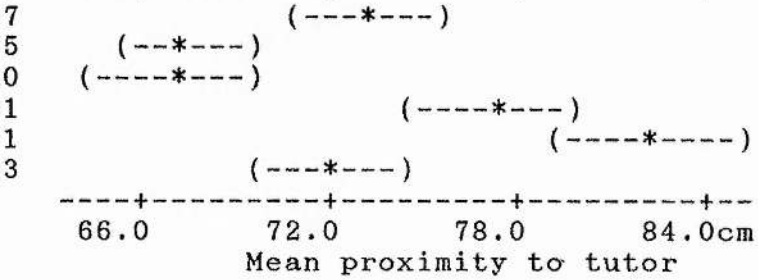
Cage	N	MEAN	STDEV
1a	243	73.46	22.74
1b	159	69.07	17.66
2	161	77.06	14.86
3	160	80.66	20.74
4	119	77.58	20.54
5	120	68.55	14.52



Mean proximity to tutor

PERIOD C: 55-66 DAYS

Cage	N	MEAN	STDEV
1a	241	73.23	21.07
1b	271	67.49	19.75
2	165	66.95	18.20
3	199	77.15	20.01
4	152	82.04	22.01
5	269	71.83	13.93



Mean proximity to tutor

In each of the six cases above, there was a highly significant difference between the means (using analysis of variance, $p < 001$).

Table 6.16 Is there a strong correlation between proximity and song learning performance in a particular period of the sensitive phase?

	Period A 35-44d	Period B 45-54d	Period C 55-66d
Close tutees	-0.796	-0.063	-0.512
Distant tutees	-0.716	-0.192	-0.708

Values in the table are Pearson correlation coefficients (r), obtained by correlating the mean proximity to the tutor with the percentage of song elements copied from him. None of the values of r quite reach significance (critical value for 4df is 0.811.

(difference in "means" > 14cm: see Figure 6.6), and this bird produced the smallest proportion of the tutor's song of the group. However, if being close to the tutor is especially important at this stage, then J389 from cage 2 might have been expected to have learnt more, as he was significantly closer to the tutor than the others. This bird, though, was ranked only third in the amount learnt. In the case of the distant tutees in period A, despite the insignificant correlation overall, the best learner was the closest to the tutor, while the two worst learners were the furthest away.

It was possible that the distance that the tutees tended to be away from the partition would be partly dependent on the position of the tutor in his cage. Where tutee location is independent of the tutor's position, it could probably be assumed that there is less of an association between the tutor and tutee, perhaps resulting in less accurate learning. Table 6.17 shows that, for two of the close tutees, the distance to the partition was significantly less when the tutor was in the most proximate third of his cage. These birds were ranked one and three in terms of their song learning. In all other cases, tutor position did not have a significant effect on this aspect of tutee location and, in fact, 6/10 of these birds were on average further from the partition when the tutor was closer.

Song output varied considerably between tutors, with a mean of 24.9 to 88.9 phrases per 20 minute watch for undirected song (Table 6.18). Directed song, sung to the close tutee, ranged from 5.7 to 9.7 phrases/watch. Directed song to the

Table 6.17 Is the distance of the tutees from the partition affected by the tutor's position in his cage.

CLOSE TUTEES

Cage	Mean distance (cm) to partition: When tutor in nearest third of his cage	When tutor in furthest third of his cage	*
1a	19.21	16.97	p=0.576
1b	18.85	16.81	p=0.448
2	9.15	12.88	p=0.013
3	14.70	14.61	p=0.967
4	11.13	19.15	p=0.004
5	22.63	18.53	p=0.083

DISTANT TUTEES

Cage	Mean distance (cm) to partition: When tutor in nearest third of his cage	When tutor in furthest third of his cage	*
1a	17.81	19.35	p=0.606
1b	10.57	12.74	p=0.239
2	13.53	9.74	p=0.061
3	21.35	17.94	p=0.122
4	18.52	23.05	p=0.146
5	6.88	9.09	p=0.241

* - the probability of there being a difference in the mean distances, from analysis of variance.

Summary of above tables, with amount of song learning from the tutor shown (as a percentage):

Close tutees

Closer to partition when tutor in nearest third of his cage		Further from partition when tutor in nearest third of his cage	
SIGNIFICANT	NS	NS	SIGNIFICANT
J389 - 76.4		J212 - 61.3	
J161 - 81.7		J360 - 73.9	
		J115 - 80.6	
		J367 - 73.9	

Distant tutees

Closer to partition when tutor in nearest third of his cage		Further from partition when tutor in nearest third of his cage	
SIGNIFICANT	NS	NS	SIGNIFICANT
	J211 - 38.8	J390 - 76.4	
	J359 - 37.0	J113 - 13.9	
	J135 - 27.5		
	J368 - 41.5		

Table 6.18 Tutor song output throughout the experiment

Cage	Tutor	Number of watches	Undirected song (mean phrases/ watch)	Directed song (*) (mean phrases/ watch)
1a	T29	7	24.9	8.7
1b	T249	8	75.3	7.3
2	T506	8	57.7	5.7
3	T162	9	88.9	7.3
4	T224	6	29.3	8.9
5	T119	7	56.7	9.7

Each "watch" lasted for 40 minutes.

* - the directed song recorded was almost exclusively to the close tutee. T29 sang nine phrases to the distant tutee during one watch, but this was the only exception.

Pearson correlations between the percentage of elements copied from the tutor and:

undirected song output of tutor

	r	T	p	
Close tutees	0.448	1.00	> 0.2	NS
Distant tutees	-0.186	0.38	> 0.2	NS

directed song output of tutor

	r	T	p	
Close tutees	-0.226	0.46	> 0.2	NS
Distant tutees	-0.486	1.11	> 0.2	NS

distant tutee was only recorded during one watch, by T29, but this might be partly due to the difficulty of categorising directed song as such when the target individual is some distance away. There was no hint of a positive correlation between tutor song output and the amount of his song that was copied.

When the tutor began singing undirected song, there was a significant tendency for tutees to react by approaching, rather than moving away from the singer (Table 6.19). Close and distant tutees did not differ significantly in the strength of this approach response, but there was slight trend for more approaches by the former group. Close tutees were significantly more likely to approach when the tutor was singing undirected song than directed, but this would have been influenced greatly by the difference in the locations of the birds at the onset of the two types of tutor song. This is shown clearly by the comparison of Figure 6.7 with Figure 6.8; for the close tutees, the mean distance to the tutor was significantly less when the latter was singing directed, as opposed to undirected song (Table 6.20). Distant tutees hardly seemed to respond at all to the tutor singing to the other tutee, perhaps because the song is directed away from them at the far end of the tutor's cage.

There was no significant correlation between the amount of the tutor's song copied and the strength of the approach response (Table 6.21).

Table 6.19 The "approach" or "move away" reaction of the tutees to tutor song

Undirected song.

		Cage 1a	1b	2	3	4	5	Total
Close tutees	A	3	9	7	11	2	9	41
	M	2	2	4	6	0	5	19
Distant tutees	A	1	11	6	8	0	11	37
	M	3	9	4	7	0	6	29

Directed song.

		Cage 1a	1b	2	3	4	5	Total
Close tutees	A	1	2	1	1	0	2	7
	M	5	2	1	2	3	0	13
Distant tutees	A	0	0	0	0	0	0	0
	M	0	0	0	1	0	0	1

A = approach singing tutor
M = move away from singing tutor

Note: The third possible response to the onset of tutor song, i.e. remaining in the same position, was by far the most common. For this analysis, there were 540 bouts of undirected song observed altogether and 77 of directed song.

i) Is there a more of a tendency to approach the tutor when he starts to sing undirected song, than to move away?

Wilcoxon matched pairs test, n = 11, two-tailed:
p = 0.013, ie. there is a significant tendency to approach, across all birds.

ii) Do close and distant tutees differ in the degree of their approach response to undirected song of the tutor?

	A	M
close	41	19
dist	37	29

Chi-square = 2.007, 1 degree of freedom: p > 0.05, NS.

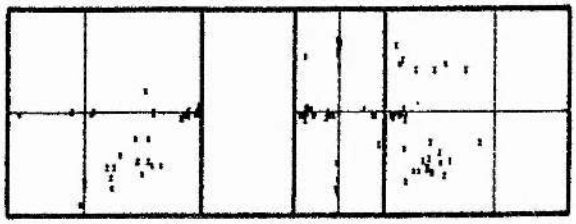
iii) Do close tutees respond differently to directed song?

	A	M
dir	7	13
undir	41	19

Chi-square = 6.94, 1 degree of freedom: p < 0.05, SIGNIFICANT.
ie. they approach more frequently when tutor singing undirectedly.

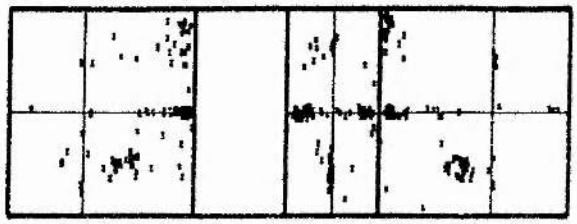
Figure 6.7 Plots of bird positions at the start of undirected song bouts by the tutors.

CAGE 1a



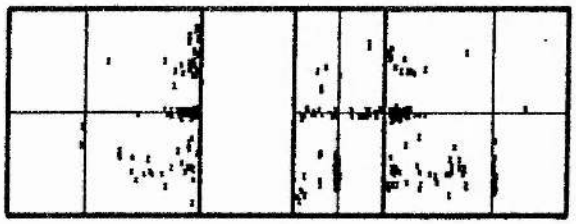
J211 T29 J212

CAGE 1b



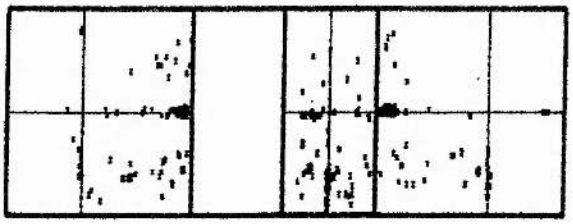
J359 T249 J360

CAGE 2



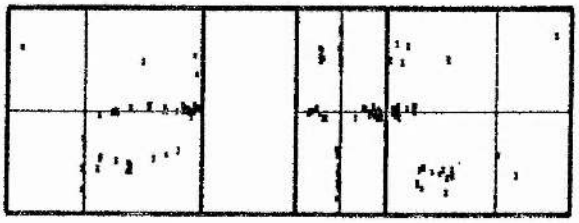
J390 T506 J389

CAGE 3



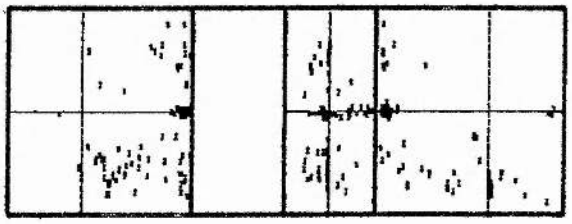
J113 T162 J115

CAGE 4



J135 T224 J161

CAGE 5.

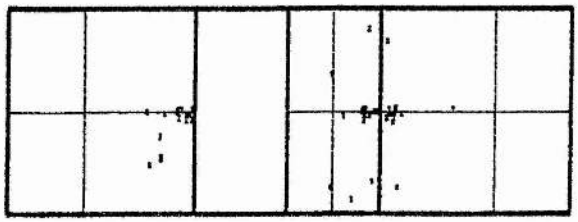


J368 T119 J367

Data from all observations.

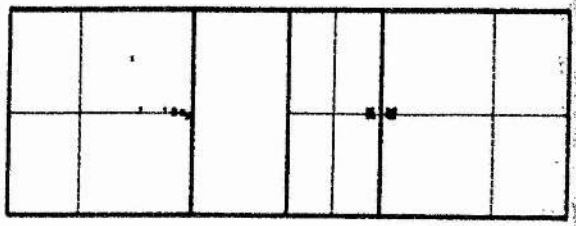
Figure 6.8 · Plots of bird positions at the start of directed song bouts by the tutors.

CAGE 1a



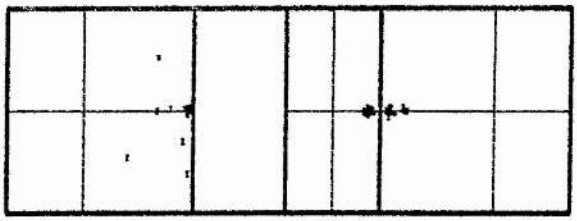
J211 T29 J212

CAGE 1b



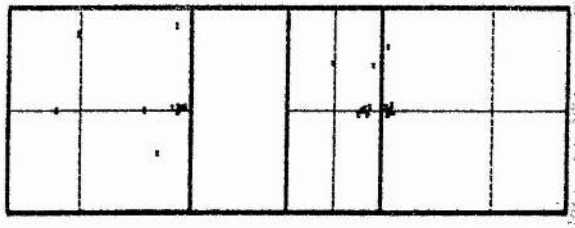
J359 T249 J360

CAGE 2



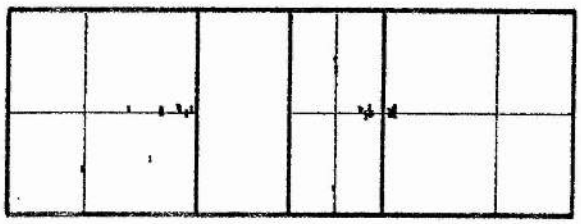
J390 T506 J389

CAGE 3



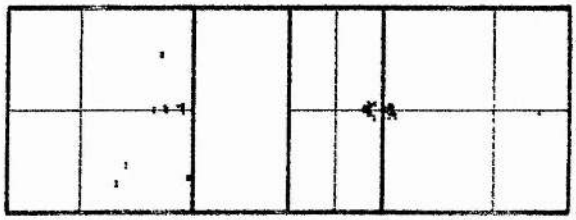
J113 T162 J115

CAGE 4



J135 T224 J161

CAGE 5



J368 T119 J367

Data from all observations.

Song was always directed to the tutee on the right (ie. the "close" tutee).

Table 6.20 The pattern of tutor-tutee proximity for the close tutees when the tutor begins to sing directed or undirected song.

Cage	Mean distance to tutor (cm): when tutor starts singing undirected song	when tutor starts singing directed song
1a	41.97	15.73
1b	42.25	8.23
2	37.57	9.79
3	39.23	11.00
4	38.86	14.08
5	41.19	13.92

Wilcoxon matched pairs test, $n = 6$, $W = 21$, $p = 0.036$.

Table 6.21 Is there a correlation between the relative number of approach responses and the song learning performance of the tutees?

	Close tutees		Distant tutees	
Cage	A:M	% of tutor's song copied	A:M	% of tutor's song copied
1a	0.60	61.3	0.25	38.8
1b	0.82	73.9	0.55	37.0
2	0.64	76.4	0.60	76.4
3	0.69	80.6	0.53	13.9
4	1.00	81.7	-	27.5
5	0.64	73.9	0.65	41.5

A:M - ratio of approaches towards tutor, versus movements away from tutor.

Close tutees: Pearson correlation coefficient $r = 0.530$, $t = 1.25$, 4 degrees of freedom: $p > 0.2$, not significant.

Distant tutees: Pearson correlation coefficient $r = 0.223$, $t = 0.46$, 3 degrees of freedom: $p > 0.2$, not significant.

Looking across both groups of tutees, there was no general tendency for tutor-tutee distance to be less when the tutor was about to sing undirected song, than on other occasions (Table 6.22). Where a significant increase or decrease did occur for a tutor-tutee pair, there was no obvious link with song learning. For example, J212, from cage 1a, was significantly closer to its tutor when a song bout started than in general, but he copied relatively little of the tutor's song.

Using the angle of orientation data, the proportion of song events in which the tutor was oriented towards the left or right tutee can be calculated. A positive (but still insignificant), correlation was obtained only when these data were compared with the amount of song copied for the close tutees (Table 6.23).

The time of onset, and relative amount of subsinging by the juveniles before 65 days, could relate to song learning. As distant tutees developed songs of poorer quality, it was possible that they also started to subsing later, but this turned out not to be true (they started earlier in three out of five cases). The amount of subsinging in period C (55 to 66 days) tended to be higher in the close tutees, though it was not significantly so, probably largely due to the small data set (Table 6.24); however, within each group subsong seemed little related to song learning (for example, the two close tutees that copied most from the tutor sang relatively little).

Table 6.22 Is the proximity to tutor different than usual at the moment that he starts to sing undirected song?

CLOSE TUTEES

Cage	Mean distance to tutor (cm): when tutor not singing	when tutor starts to sing	Distance greater or less at onset of song	
1a	46.17	34.47	LESS	p<0.001
1b	43.22	39.45	less	p=0.066
2	30.78	34.94	GREATER	p=0.011
3	36.75	36.16	less	p=0.787
4	40.41	33.21	LESS	p=0.023
5	40.00	38.08	less	p=0.394

DISTANT TUTEES

Cage	Mean distance to tutor (cm): when tutor not singing	when tutor starts to sing	Distance greater or less at onset of song	
1a	72.83	76.31	greater	p=0.251
1b	69.55	73.10	GREATER	p=0.034
2	70.66	65.94	LESS	p=0.001
3	77.76	74.95	less	p=0.182
4	80.41	78.46	less	p=0.501
5	70.72	75.12	GREATER	p=0.004

The probability scores in the above tables were obtained by using analyses of variance. The use of upper case with the word "greater" or "less" serves to emphasise the significant differences within individuals.

If we look across the whole of each group, we find that there is no overall tendency for either an increase or decrease in tutor-tutee distance, when the tutor starts to sing. (For close tutees: Wilcoxon matched pairs test, $n = 6$, $W = 17$, $p = 0.208$. For distant tutees: $n = 6$, $W = 9$, $p = 0.834$).

Table 6.23 Correlation between the amount of time the singing tutor spent facing towards each tutee, and the amount of his song that was learnt.

Cage	Close tutees		Distant tutees	
	%R	% of tutor's song copied	%L	% of tutor's song copied
1a	25.8	61.3	39.4	38.8
1b	33.3	73.9	15.6	37.0
2	24.2	76.4	25.8	76.4
3	30.6	80.6	16.7	13.9
4	52.9	81.7	11.8	27.5
5	31.1	73.9	18.4	41.5

%R - the percentage of song events in which the tutor was oriented towards the right-hand (close) tutee (angle 300-060°).
%L - the percentage of song events in which the tutor was oriented towards the left-hand (distant) tutee (angle 120-240°).
Close tutees: Pearson correlation coefficient r = 0.550, t = 1.32, 4 degrees of freedom: NS

Distant tutees: Pearson correlation coefficient r = - 0.378, t = 0.817, 4 degrees of freedom: NS

Table 6.24 The rate of subsinging of the tutees between 55 and 66 days.

	Rate of subsinging (*) by:	
Cage	Close tutee	Distant tutee
1b	0.27	0.21
2	0.07	0.05
3	0.05	0.02
4	0.07	0.07
5	0.34	0.01

Wilcoxon matched pairs test, n for test = 4, two-tailed, W = 10, p = 0.10.

* - Rate of subsinging calculated as [number of minutes in which subsinging occurred]/[number of minutes sampled]

The occurrence of subsinging was not recorded for the tutees from cage 1a.

Significant differences were found in the activity scores of the various tutors and tutees (Figure 6.9). Such data could reflect levels of stimulation: juveniles with their attention directed obviously towards the tutor, often hop persistently to-and-fro along the end of the cage, sometimes repeatedly flying up onto the wire partition. Even so, there was no hint at all that such a broad measure of activity can give an indication as to the song learning proficiency of the juveniles. In fact, a significant negative correlation resulted, when tutor activity was compared with the amount of song copied by the distant tutee.

An interesting aspect of this set of data was the strong matching of activity scores between the pairs of tutees, across all cages except 5 (where J367, the close tutee, was far less active than J368).

6.4 Discussion

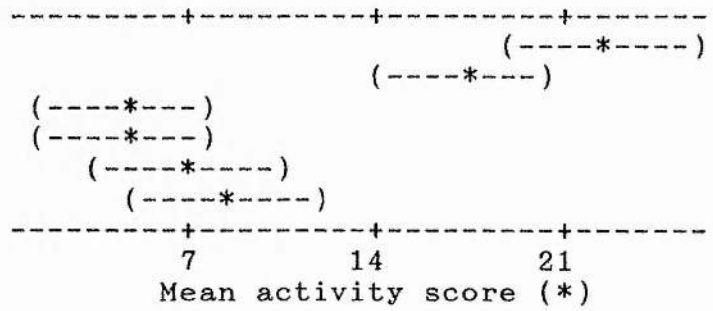
In this experiment, I have looked at the learning differences that exist between tutees housed adjacent to a tutor and others housed with a small gap of 38cm interposed. I have also looked for correlations with behavioural data, and with more precise measures of proximity.

In theory, there are various ways in which such a gap could inhibit song learning. Firstly, it might almost completely disallow certain interactions important in song tutor selection; for example, aggression from the tutor is effectively prevented, as is close bonding (and the

Figure 6.9 The locomotor activity of the experimental birds, and its possible relationship with song learning.

i) Tutor activity.

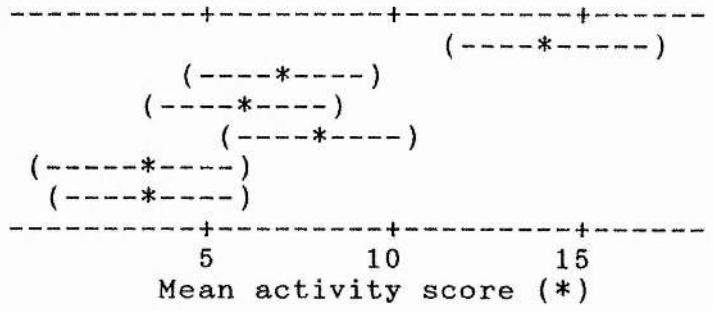
Cage	N	MEAN	STDEV
1a	12	22.2	9.0
1b	16	17.3	8.4
2	14	4.7	5.1
3	14	4.6	3.0
4	11	7.0	4.6
5	13	8.3	4.5



Analysis of variance, 5 degrees of freedom, F = 18.15:
p < 0.001, SIGNIFICANT.

ii) Activity of close tutees.

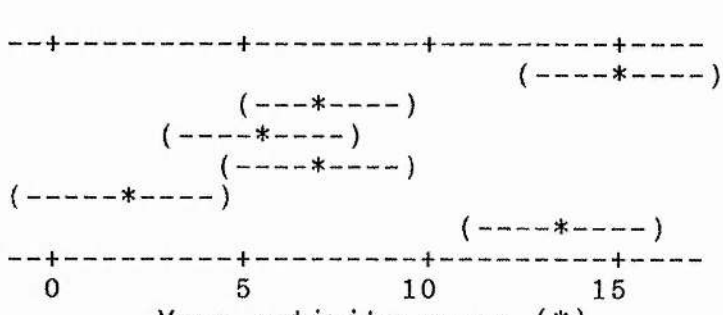
Cage	N	MEAN	STDEV
1a	12	14.1	9.6
1b	16	7.0	3.8
2	14	6.1	4.5
3	14	8.1	3.2
4	11	3.3	2.8
5	13	3.5	1.7



Analysis of variance, 5 degrees of freedom, F = 8.04:
p < 0.001, SIGNIFICANT.

iii) Activity of distant tutees.

Cage	N	MEAN	STDEV
1a	12	15.1	6.8
1b	16	7.1	3.7
2	14	5.4	4.5
3	14	7.0	4.6
4	11	2.0	1.1
5	13	13.5	4.8



Analysis of variance, 5 degrees of freedom, F = 14.43:
p < 0.001, SIGNIFICANT.

* - the activity score is the mean count per minute of the number of changes in perch position (see Methods).

Figure 6.9 (continued)

Correlation between the levels of tutor activity, and the song learning performance (% of tutor's song copied) of the close tutees:

$r = -0.858$, $t = 3.34$, $df = 4$, $p < 0.05$*

Correlation between the levels of tutor activity, and the song learning performance (% of tutor's song copied) of the distant tutees:

$r = -0.063$, $t = 0.12$, $df = 4$, $p > 0.5$

Correlation between the activity scores of the close tutees and the amount of the tutors' songs copied:

$r = -0.783$, $t = 2.52$, $df = 4$, $p > 0.05$

Correlation between the activity scores of the distant tutees and the amount of the tutors' songs copied:

$r = 0.019$, $t = 0.04$, $df = 4$, $p > 0.8$

Correlation between the levels of tutor activity, and the activity levels of the close tutees:

$r = 0.705$, $t = 1.99$, $df = 4$, $p > 0.1$

Correlation between the levels of tutor activity, and the activity levels of the distant tutees:

$r = 0.583$, $t = 1.44$, $df = 4$, $p > 0.2$

Correlation between the levels of activity of the close and distant tutees:

$r = 0.555$, $t = 1.33$, $df = 4$, $p > 0.2$

Correlation between the levels of activity of the close and distant tutees, excluding cage 5:

$r = 0.994$, $t = 18.18$, $df = 3$, $p < 0.002$*

associated clumping and allopreening). Although these are also severely restricted for close tutees, separated from a tutor by a mesh partition, they can nevertheless still occur to a limited extent - birds have been observed preening each other through the wire mesh, and will sometimes sit side by side on either side of the partition. Secondly, as well as these qualitative differences that can exist between distant and close tutees, there may also be differences in quantity. That is, accurate song learning may be possible despite the 38 cm separation, but may be less likely than for close tutees because certain kinds of interaction occur less frequently, or because the distance results in the tutor's behaviour arousing the tutee's interest less often.

If certain interactions that cannot take place across a physical gap are very important in song tutoring, then the distant tutees would all be expected to learn approximately equally badly. However, with quantitative differences, significant effects are likely to arise in the amount of song that these tutees manage to copy from the tutor, dependent on: i) the behaviour of the tutee, ii) the behaviour of the tutor, iii) the interactions between the two of them. The *actual* distance apart will probably affect these, so proximity could well relate to learning performance.

First of all, it *was* found that the distant tutees learnt less well than the close tutees. If raised by both parents, they copied relatively fewer elements from their tutors and more from their fathers. If female-raised, they tended to

"improvise" more song. Also, in two cases, distant tutees failed to acquire a song phrase that fell within the normal range in its consistency of patterning.

Despite this result, distant tutees did not fail to learn tutor's songs completely - one even copied 76.4% of it. Their performance was better than occurred in Adret's experiment with the imposed 50cm gap. The reasons for this difference could be that:

1) The shorter gap of 38cm was insufficient to cause a complete block on learning, or

2) The decision to use a linear arrangement of cages may have resulted in the attention of the distant tutee being more strongly directed towards the tutor, because it could see two birds, *that were able to interact with one another*, and not just one. This effect might have been enhanced by the fact that the other tutee was a sibling. An indication that they may still have been quite attentive to each other comes from the very similar activity scores of most of the pairs of brothers.

3) Another significant factor may have been that juveniles in Adret's matrix were unlikely to have received as much individual attention from the tutor, because there were nine young birds to one adult, instead of two to one.

The pattern of results, with birds varying considerably in the amount of song that they copied, meant that we could look for behavioural factors that might explain the within-group, as well as between-group, differences.

Several measures of proximity were compared with song learning performance, but in no case did significant correlations with song learning result (although there were significant differences in the proximity measures within the close and distant tutee groups). However, the correlations did tend to be in the same direction, with birds at the extremes of learning performance being generally at the predicted end of the proximity rankings. The possibility that close proximity might only be of great importance during a short period within the 30 days could be neither confidently upheld nor dismissed, although for both sets of tutees the correlations with the amount of song copied were greatest in the 35 to 44 day period.

There was no tendency for tutor-tutee distance to be below average when the tutor started to sing. This might seem an obvious finding because, at the start of a song bout, the tutees can hardly be expected to have reacted to the singer. However, it could have been that tutors sang more often when a particular tutee was close, or that a preceding song bout by the tutor encourages juvenile approach and that a second bout often occurs while the latter is still nearby. Furthermore, as tutees usually did not move position following the onset of tutor song, their proximity at the start of a bout is likely to be a good predictor of that during.

The tutors involved in the experiment all had song outputs in the normal range and so, as expected, this factor did not influence the amount of song copied (there is some evidence

that individuals singing particularly infrequently might be avoided as song models, Böhner 1983, Slater et al 1991). "Directed song" was only recorded, with one exception, from the tutor to the close tutee. This is therefore a qualitative difference between the interactions that the close and distant tutees were involved in. As directed song occurs mostly at very close range (as shown clearly on Figure 6.7), the strong stimulus provided by song in these circumstances may facilitate song learning, and at least partly account for the discrepancy in performance between close and distant birds. Why the tutor should sing directedly at all to a male tutee is not clear, as this song is considered to have a courtship function (but directed song to males may be functionally, and structurally, distinct, Walters et al 1991). Part of the reason could be due to tutees not possessing fully developed male plumage features, at least at the start of the tutoring period. It could also be an example of mis-directed sexual behaviour, brought about by the artificial constraints of the experiment (in addition to directed song, persistent bill-wiping, another courtship behaviour, was noted between tutors and tutees). Homosexual behaviour has been described in zebra finches before by Morris (1954), and was also evident in the aviary experiment of this thesis (Chapter 5). Our main hope of finding an explanation for the song copying differences lay with the close observation of tutee reaction to song. Unfortunately, some behaviour patterns, that might be important, proved impossible to record in a sufficiently objective fashion. For example, an alert, upright posture was often adopted at the onset of song, by a bird previously

in a resting position. This could have been the listening behaviour described for juvenile zebra finches in the presence of Bengalese finch tutors (ten Cate 1986a). Similar apparent attentiveness by young males to a singing tutor was seen by Adret (pers.comm), in his observations on blind-folded zebra finches. The difficulty was that such a body posture is hard to define and categorise objectively.

In contrast, whether the tutees approached, or moved away from the tutor when he began to sing was relatively easy to note. Here we found that approaching was more common than retreating, and this perhaps more so with the close tutees. If the latter represents a genuine difference, then it may be representative of the close tutee's greater attentiveness to the tutor, resulting from his greater proximity.

The orientation of the singing tutor did not provide a clear clue to the subsequent copying performance of the tutees. However, there was the usual hint of a pattern: the close tutee that learnt the most had the tutor that spent the greatest proportion of time facing towards him while singing. Also, in two cases the tutor actually spent more time facing the distant tutees while singing, and these were ranked first and third in terms of their song learning. It is likely that the formation of some sort of social bond between an adult and juvenile male facilitates song learning, for example where the tutor directs song to the tutee. If so, we might expect song learning to be more complete where the finches were most highly synchronised in behaviour. It was found that the tutors' activity scores

correlated more with those of the close tutees than with those of the distant tutees, although neither reached significance. Also, in two cages there was a significant tendency for a tutee to be nearer to the partition when the tutor was close to it, and the birds in these cases were among the best learners of the close tutees.

Neither the timing of onset nor the quantity of juvenile subsong seemed to relate to the extent of song learning. For example, one of the two distant tutees which had very low phrase consistency scores (J135 from cage 4) was subsinging from 56 days (earlier than recorded for its brother) and sang relatively frequently in period C compared to other distant tutees, and as much or more than three of the close tutees. This suggests that poor song stimulation in the sensitive phase may not delay the onset of the process of song production, but may instead retard its progress.

To conclude, a 38cm gap did prove enough to inhibit song learning from a tutor during the sensitive phase. Why this should be so is still not certain, but it is likely to be due to a combination of factors. Whether or not a tutee will learn the song probably depends on its attentiveness to the tutor, or on how responsive it is to the tutor's behaviour. These factors will both be affected by proximity to the tutor, such that measures of tutor-tutee proximity should correlate with the amount of learning that takes place. That this was not convincingly the case in the present experiment is probably due to the small sample size, or to the presence or absence of certain behavioural interactions that can

occur independently, to some degree, of proximity. For example, the responsiveness of the tutee might be raised by aggressive attacks, or courtship, from the tutor, or by other aspects of social bonding. Perhaps song learning might even be possible across Adret's 50cm gap, provided that the level of stimulation provided by the tutor is elevated in some way (perhaps by housing a female with him).

Appendix 6.1 Defining zebra finch song elements

To determine how much of a tutor's song a young Zebra Finch has learnt, sonagrams of their vocalisations are usually compared by eye. The method simply involves "breaking down" the phrases into small units ("elements"), and then calculating the percentage of tutor song elements that has been copied (or alternatively, the percentage of a tutee's song derived from the tutor).

There is a problem here, however, with element definition. An element is usually defined as a *temporally-distinct* unit of song (e.g. Sossinka and Böhner 1980). This is fine for most purposes: most experimental regimes have resulted in either extensive or very little learning from a particular tutor, so that points of detail in definitions do not matter much. Even if some parts of a song did not split neatly into elements as defined above, the overall result (whatever the compromise) would be unaffected. The difficulty arises in studies such as the present one, where the questions such as "did X learn *more* of the tutor's song than did Y?" need to be answered. In this case, we need to be sure that a difference arising fom our element count-up is genuinely representative of a difference in learning performance.

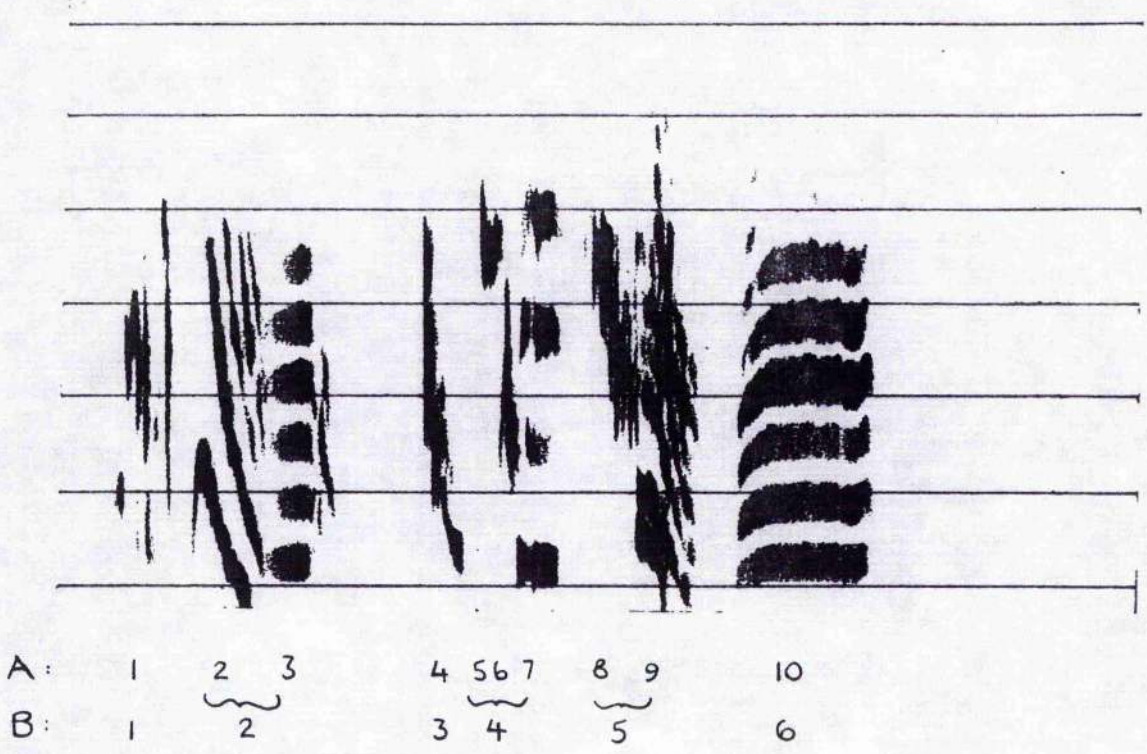
The main problem is with "compound elements"; that is, elements formed of two or more sound structures which are not, however, temporally distinct. Quite often, only part of a tutor's compound element is copied, or a young bird will possess a compound element that is part copied, part

improvised. In the first case above, we could score the young finch as having copied only a half (or third etc.) of an element, but this assumes that the birds are perceiving units of song in the same way that we are. It could equally be that two parts of a compound element are perceived as being fully discrete; copying both may well be equivalent to to copying two "standard" elements.

There is an argument, therefore, for an alternative element definition, as follows:
An element is a temporally-distinct unit within the song phrase, unless there are two or more quite different sound structures within this unit, in which case each is classified as a separate element.

Figure 6.10 shows how the same song phrase can be labelled quite differently, using the two definitions.
Using the second definition, A2 and A3 must be considered as being separate, as they are clearly of quite different structure. Classification is not always so straightforward. "Chevron" structures, usually of high frequency, are common in Zebra Finch songs. Where the chevron is complete, it is easily classified as a single element. However, sometimes there is a split (A5 and A6). To label as one or two elements in such a case requires scrutiny of numerous sonagrams of the structure: sometimes the split is an artefact, resulting from too much attenuation during recording or sonagramming. "Noisy" structures (A1 and A8) consist of a series of vertical lines on a sonagram. The lines may be temporally distinct, but there is no change in

Figure 6.10 Labelling song elements using the two element definitions : an example, using a typical zebra finch song phrase.



A - elements labelled following the new definition given in Appendix 6.1.

B - elements labelled using the standard element definition (eg. Sossinka & Böhner 1980).

the sound structure, so they are not split into several elements.

A special case is the male distance call. Although comprised of a tonal and then a frequency-modulated part, it is almost always copied as a discrete unit. Also, splitting the two components would frequently prove unworkable, as the transition between them is often not strongly demarcated. For both reasons distance calls are best regarded as being single elements. (On the rare occasions that such a note *is* split by a tutee, then it must also be split in the tutor).

Appendix 6.2

It could be hypothesised that close tutees would match the tutors more closely than the distant tutees in phrase length, pause length (between phrases) and tempo; however, it was decided that these might be misleading measures. Phrase length and tempo are strongly affected by the precise structure of the elements contained in the song. An attempt to match such song characteristics could easily be obscured by the failure to copy just one tutor element if, for example, that element happens to be of particularly long duration.

Furthermore, all three characteristics, even within undirected song, may be affected to some degree by the motivational state of the bird being recorded.

Appendix 6.3 Sonagrams of all birds involved in Chapter 6

Representative sonagrams are shown. In cases where phrase consistency was particularly low (e.g. J359 and J135), not all elements are depicted.

The elements of the tutors and fathers are numbered (in Roman numerals, in the latter case). Juvenile elements that seemed to have been copied from these are labelled with the corresponding number.

Miscellaneous comments about features of the juvenile songs:

Cage 1b. Element A of J360 is used as an introductory element, but is not typical of notes used for this purpose. Element 3 from the tutor's song was copied by J360, but is not depicted on the sonagram for the juvenile. Elements B and C of J359 are variable in duration and, in the case of B, also in structure. The group of elements labelled "D" are poorly defined and inconsistent in their order and frequency of usage.

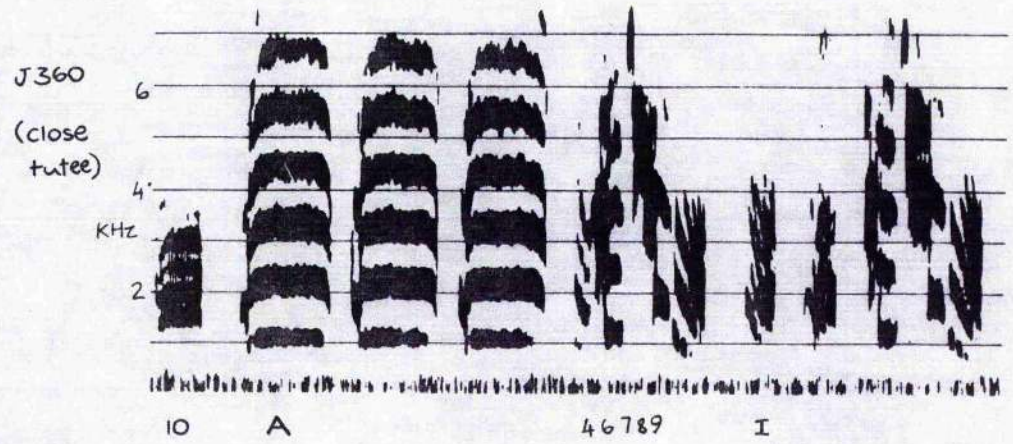
Cage 2. Many of the elements of J390 are poorly defined.

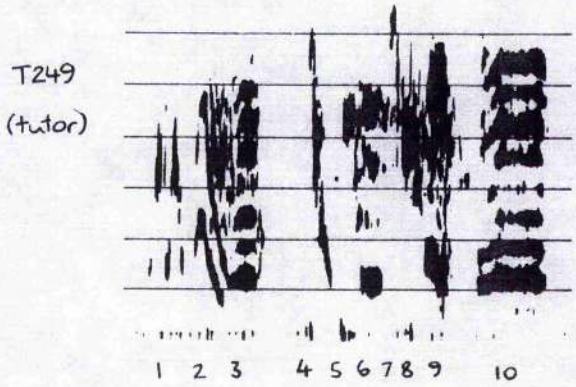
Cage 1a. J211 copied element "iv" from F165, but this element is not shown.The song of J211 was relatively undeveloped. It was particularly unstereotypic and possessed elements that were inconsistent in form (especially the copy of element 5 from T29).

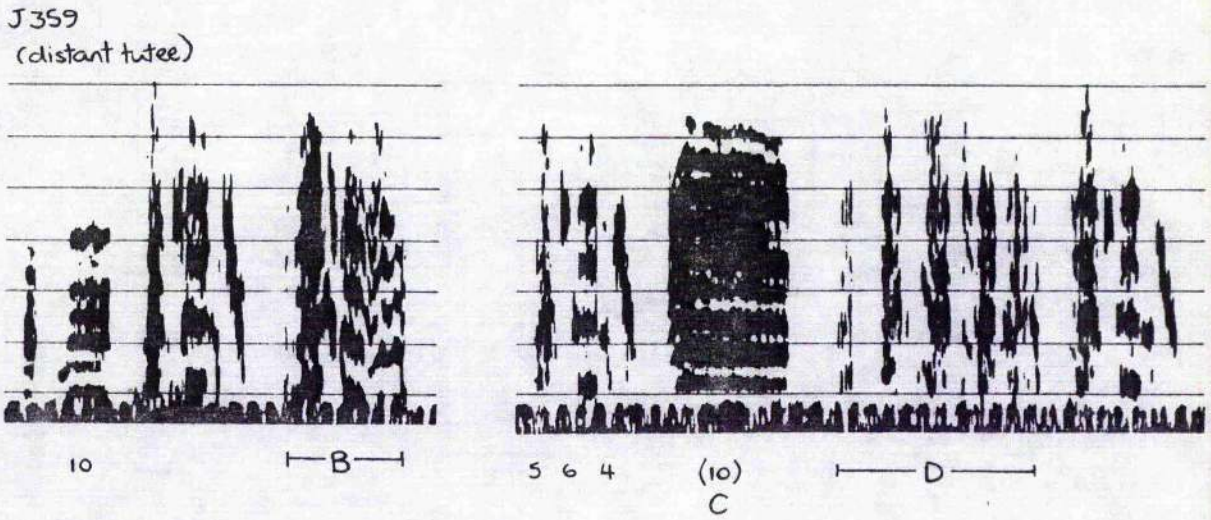
Cage 4. It was quite obvious from their order and context that elements 1 to 5 from T224 had been copied from J161. However the accuracy of copying was relatively poor. Similarly this bird produced a poor copy of element "i" from F60. The song of J135 lacked normal phraseology and contained some very variable elements. The distance call element, H, is of unusually long duration.

APPENDIX 6.3 Sonagrams of birds involved in Chapter 6

a) Female-raised young. CAGE 1b.

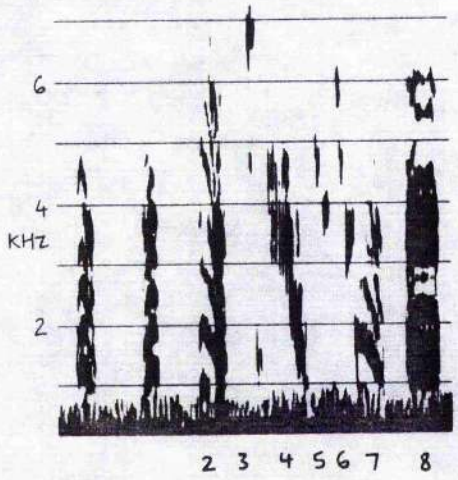




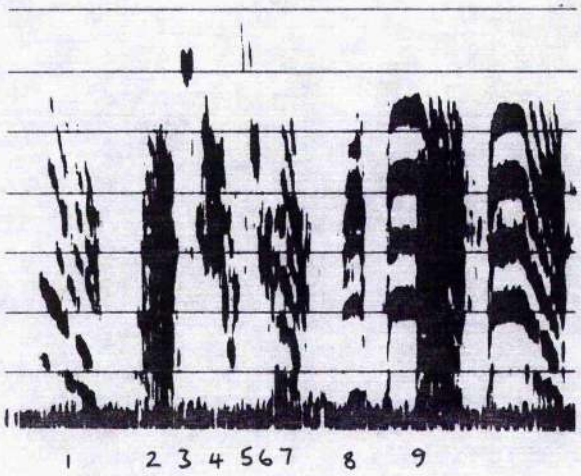


Female-raised young CAGE 2

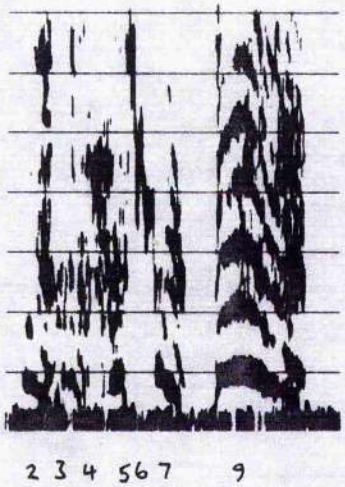
J389
(close
tutee)



T506
(tutor)

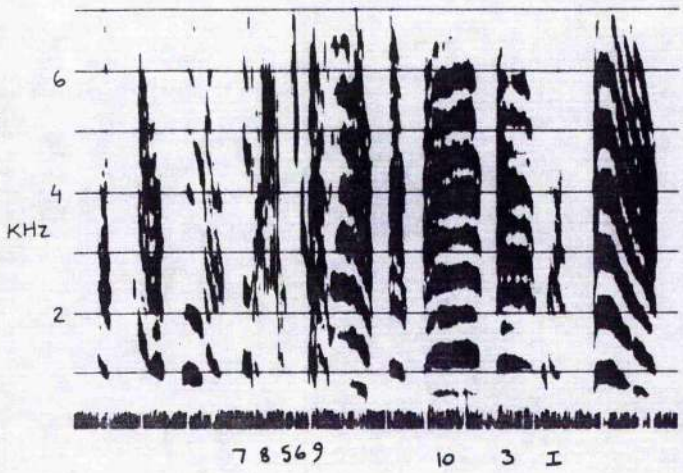


J390
(distant
tutee)

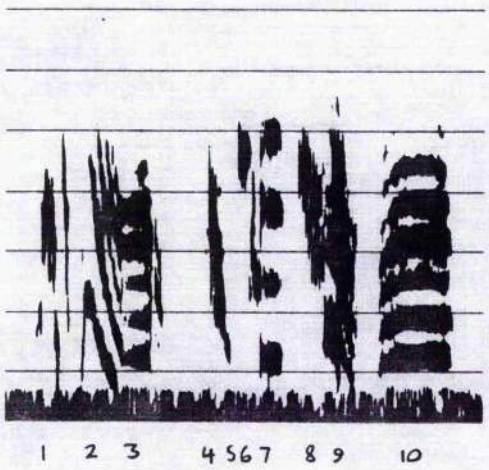


Female-raised young CAGE 5

J367
(close
tutee)

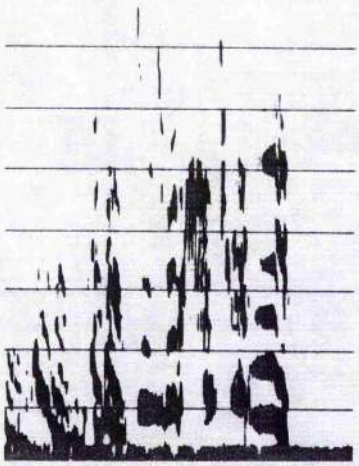


T119
(tutor)

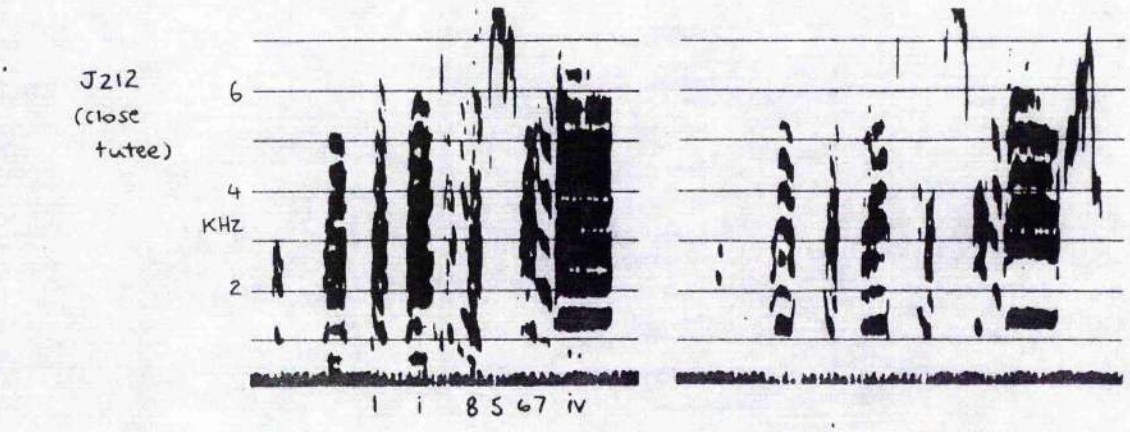


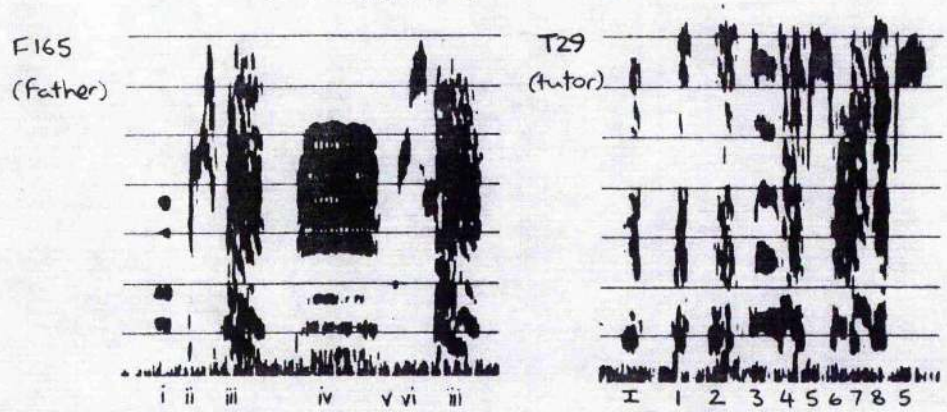
Not shown:
Introductory note (I),
copied by J367.

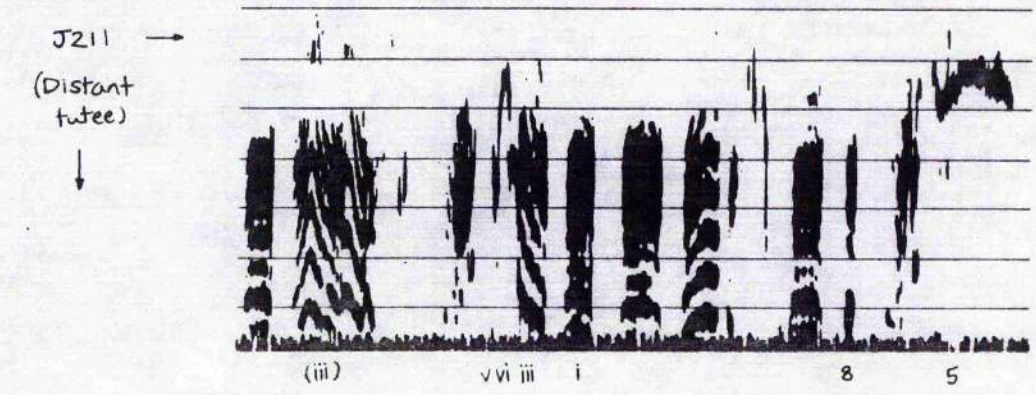
J368
(Distant
tutee)

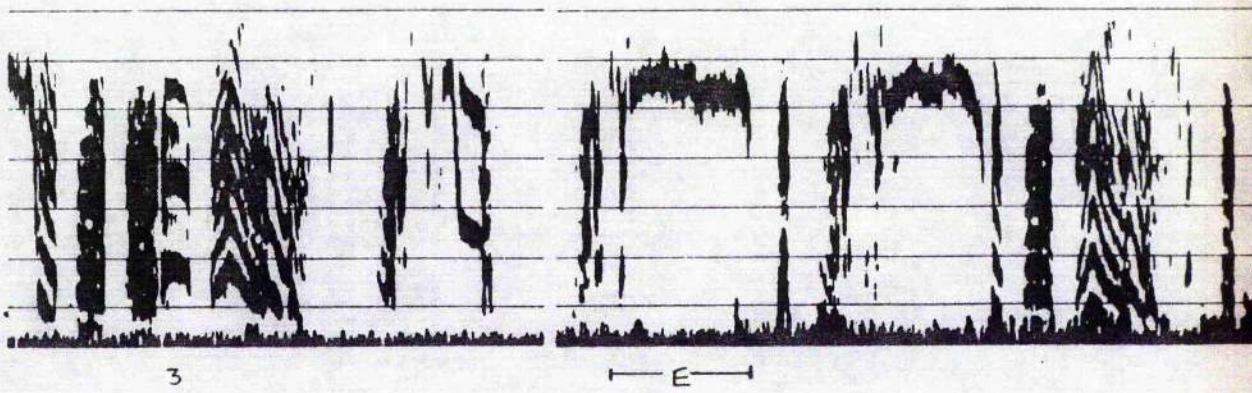


b) Normally-raised young CAGE 1a



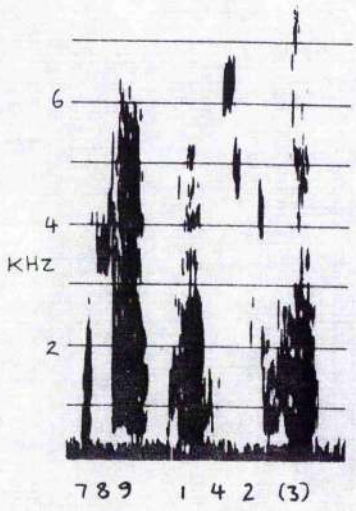




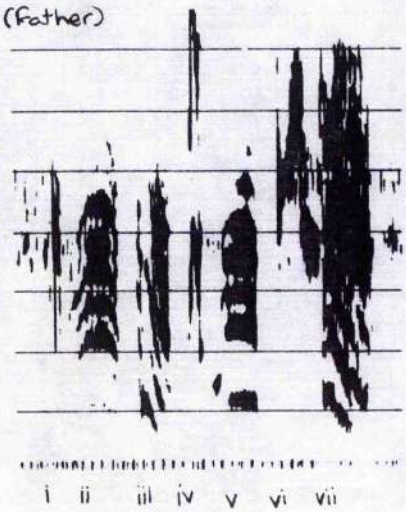


Normally-raised young CAGE 3

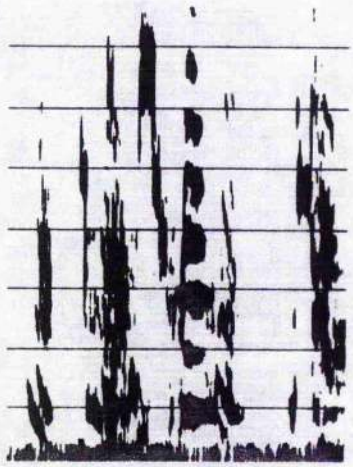
J115
(close
tutee)



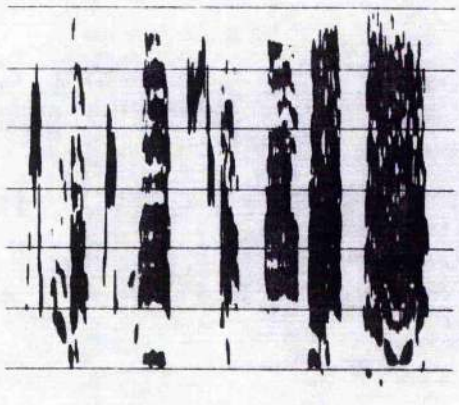
F78
(Father)



T162
(tutor)

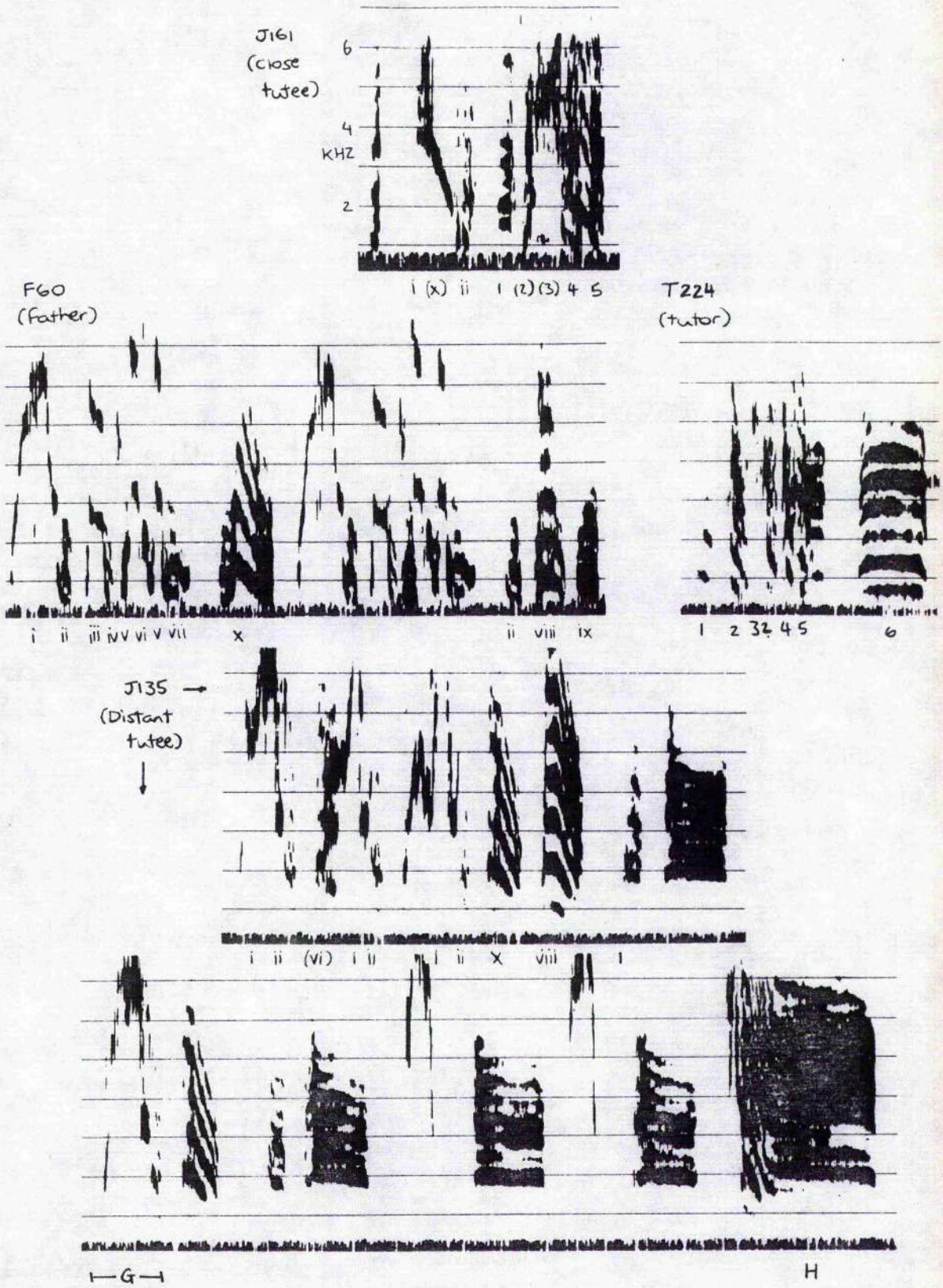


J113
(distant
tutee)



F

Normally-raised young CAGE 4



CHAPTER 7: GENERAL CONCLUSIONS

The main aims of this thesis have been to identify factors that can direct song tutor choice in zebra finches and then to put these, and the other known influences, into a more general context so that the process of song tutor selection can be better understood.

There has been some disagreement with regard to people's views on the outcome of song tutor choice in the wild (reviewed by Slater and Mann 1990). This has been for two main reasons. Firstly, it is particularly difficult to follow the course of zebra finch song learning in a wild population, not least because of the gregarious nature of the species, and the consequently high number of potential tutors. Secondly, song tutor choice, as shown from laboratory work, is a finely balanced process, often affected greatly by subtle changes in experimental design.

However, certain patterns are now becoming clear. Working in the field, Zann (1990) has shown, at least in his population, that fathers and sons have more similar songs than would be expected by chance. This suggests either direct copying, or a preference for a tutor with a song resembling that of the father (as has been shown to occur in the laboratory, Clayton 1987b); both seem equally plausible. Probably only a complete knowledge of the songs in a study population would allow a distinction to be made between the two possibilities, unless a

method for following the associations of the juveniles can be successfully implemented.

A logical step from this finding of Zann's is to attempt to put forward functional reasons for having a song like that of the father. It could be that this provides a mechanism by which optimal outbreeding can be achieved, if females choose males as mates that have songs differing to a particular extent from those of their fathers (Slater et al 1988, Zann 1990; also see Bateson 1983). However, evidence concerning this aspect of female sexual preference is lacking at present. That females prefer to perch near to a loud speaker playing their father's song, rather than to one playing the song of a stranger (Miller 1979a) does not necessarily imply sexual motivation.

Directed song does undoubtedly have a sexual function in the species (e.g. Sossinka and Böhner 1980); for example it is frequently a precursor to mating and occurs principally from an adult male to his mate. Even so, all that may matter in terms of female arousal, is that the male has a song possessing species-specific characteristics. The precise construction of the song, in terms of its component elements for example, may matter little. Acquiring a species-specific song could be achieved with a relatively passive process, by learning from a bird, or birds, to whom exposure is greatest. This may well lead, in most cases, to juveniles learning their father's song. The point being made is that it requires no argument for there being direct selective pressure for learning specifically from the father.

There would be little risk of learning from the "wrong" species with this passive mechanism of tutor choice, because the strong social preference for conspecifics would ensure that there would always be greater exposure to other zebra finches.

Such a situation would fit well with the results of this thesis. Copying preferentially from a bird of the parental morph (Chapter 2) would be easily explained by imprinting directing attention mostly towards a male of the familiar colour. In Chapter 4, the preference for learning from the father was surprisingly not stronger than for an unrelated male, when the latter was housed with the mother. In fact, when the father was housed alone, experiment 2, the unrelated male (with the mother) was actually preferred as the song model. These results can be explained by the attention of the young males being divided between the two parents, so that there was substantial exposure to the unrelated male. In experiment 2 the balance of the tutee's attention may have swung towards the male housed with the mother, perhaps because of a preference for associating with a "group", or because of the type of interactions occurring between them.

In the aviary experiment, Chapter 5, no particular behaviour seemed to correlate with tutor choice. It is possible that causal reasons for each bird's choice of tutor (which could include aggressive or social behaviour, for example) varied from one individual to another, but with the similar result of drawing the juveniles attention. Relative proximity with adult males linked with tutor choice, suggesting further that the amount of exposure to a tutor may be a cause of song learning.

In the distance experiment, Chapter 6, learning was relatively weak from some tutees housed only 38 cm from the tutor, despite the latter being the only song model available. This may be an indication that, to facilitate song learning, close interactions between tutor and tutee must be possible and that these were largely prevented in this case.

Of course much of this is hypothetical. Perhaps zebra finches do actively seek out specific song tutors to copy from. This would fit with the listening behaviour observed by ten Cate (1986a) and could also be the reason for the correlations with proximity (Chapter 5) and aggression (Clayton 1987b). The point is that it is not necessary, bearing in mind our present knowledge of song learning in zebra finches, to propose any functional reason for the choice of a specific category of tutor. If achieving a species-specific song is sufficient then a system in which song is simply copied from any bird to whom exposure is greatest, is just as viable.

There are several more specific issues raised by the thesis. Chapter 2 further demonstrated that learning can occur before or after the sensitive phase if the tutor provided is in some way inadequate (in this case because he was not of the parental morph). Both Chapters 2 and 3 showed that mate preference, in terms of colour morph did not necessarily follow the same pattern as that of song tutor choice. However, this does not prove that different learning processes were involved in directing these preferences. The difference in outcome could

simply be a reflection of how variation in model behaviour can distorting an underlying preference.

In the mixed morph study, it was found that both parents influenced the song tutor and mate choice of males, and also that females are guided in mate choice by their early experience (contrary to Walter 1973). It was not possible to show clearly whether one parent has a greater impact than the other - a more rigorous experimental design would be needed to demonstate this, but interpretative problems would nevertheless be difficult to avoid.

In Chapter 3, there were indications of a preference for:
1. The father. 2. A tutor housed with the mother (not necessarily the father). 3. A paired male.
Further tests are needed to confirm, and to assess the relative strength of, these preferences.

Chapter 5, apart from revealing a general link between the proximity to a tutor and the likelihood of song copying, raised a variety of interesting points. First of all, the song learning outcome was quite different than that found by Williams (1990) and it seems that this stemmed from differences in bird density. There was relatively less space in her aviary, probably resulting in the crêching that she observed. In turn this reduced the parent-offspring contact and will thus have directed song learning away from the father. Such pronounced crêching ws not evident in my study, and correspondingly more birds copied from the father. Also birds in my aviary seemed to produce songs copied from fewer individuals, again probably

resulting from the less crowded conditions. Of particular note was the general pattern of siblings remaining in cohesive units after becoming independent, such that they occupied and defended nest sites together. These sibling groups tended to stay together until sexual pair bonds with other birds were established.

As a final comment, it is probably not possible to make a specific statement about how a male zebra finch selects its song tutor. The process of tutor choice is evidently very flexible, and can be affected by numerous factors relating to tutor-tutee behaviour. Further exploration of the female influence on male song learning is being carried out at present at St. Andrews (Slater, Jones and Povey in prep.), and will help to answer some of the points raised above. In particular, do females exhibit sexual preferences for any features of zebra finch song and is there any evidence that song learning behaviour of males has evolved so that such attractive songs are more likely to be learnt? It may of course be that females prefer features that are more representative of a male's current state of health, such as song rate. Optimal outbreeding would require no preference for a particular song feature; it would be interesting to know if the preference demonstrated by Miller (1979a) is really a sexual one.

It would also be worth looking closer at tutor-tutee interactions to try to discover whether song learning is an active or passive process. Certain observations have suggested the former - for example, listening behaviour (ten Cate 1986a),

key pressing for exposure to song (Adret, in prep.) and the tendency to approach, rather than move away from, a singing male in Chapter 6. The way in which young birds usually react to song from an adult male can be investigated in more detail - it would be particularly interesting to know whether there is a tendency for juveniles in an aviary to preferentially approach their selected song tutor when he is singing.

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour 49, 227-267.

Baptista, L. F. 1975. Song dialects and demes in sedentary populations of the white-crowned sparrow (*Zonotrichia leucophrys nuttalli*). Publ. Zool. Univ. Calif. 105, 1-52.

Baptista, L. F. & Petrinovich, L. 1984. Social interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow. Anim. Behav. 32, 172-181.

Baptista, L. F. & Petrinovich, L. 1986. Song development in the white-crowned sparrow: social factors and sex differences. Anim. Behav. 34, 1359-1371.

Bateson, P. 1978a. Sexual imprinting and optimal outbreeding. Nature 273, 659-660.

Bateson, P. 1978b. Early experience and sexual preferences. In: Biological Determinants of Sexual Behaviour Ed. J.B.Hutchison. Wiley, London.

Bateson, P. 1979. How do sensitive periods arise and what are they for?. Anim. Behav. 27, 470-486.

Bateson, P. 1983. The interpretation of sensitive periods. In: The behaviour of human infants Ed. Oliverio & Zappella. Plenum Press.

Bateson, P. 1987. Imprinting as a process of competitive exclusion. In: Imprinting and cortical plasticity. Ed. Rauschecker & Marler. Wiley, NY.

Birkhead, T. R., Pellat, J. & Hunter, F. M. 1988 . Extra-pair copulation and sperm competition in the zebra finch. Nature 334, 60-62.

Böhner, J. 1983. Song learning in the zebra finch (*Taeniopygia guttata*): selectivity in the choice of a tutor and accuracy of song copies. Anim. Behav. 31, 231-237.

Böhner, J. 1986. Der zeitliche Verlauf des Gesangerwerbs biem Zebrafinken (*Taeniopygia guttata*). Verh. Dtsch. Zool. Ges.79.

Böhner, J. 1990. Early acquisition of song in the zebra finch, *Taeniopygia guttata*. Anim. Behav. 39, 369-374.

Bossema, I. & Kruijt, J. P. 1982. Male activity and female mate acceptance in the mallard (*Anas platyrhynchos*). Behaviour 79, 313-324.

Bottjer, S. W. & Arnold, A. P. 1984. The ontogeny of vocal learning in songbirds. In: Handbook of behavioural neurobiology. Vol. 8. Ed. EM Bass. Plenum Press.

Brindley, E. L. C. 1988. A study of distance call development in the Zebra Finch and its subsequent role in discrimination between individuals. BSc. Thesis, University of St Andrews.

Burley, N. 1986a. Sexual selection for aesthetic traits in species with biparental care. Am. Nat. 127, 415-445.

Burley, N. 1986b. Sex-ratio manipulation in color-banded populations of zebra finches. Evolution 40, 1191-1206.

Burley, N., Krantzberg & Radman, P. 1982. Influence of colour-banding on the conspecific preferences of zebra finches. Anim. Behav. 30, 444-445.

Butterfield, P.A. 1970. The pair bond in the zebra finch. In: Social behaviour in birds and mammals. Ed. J.H.Crook. Academic Press, London.

Caryl, P. G. 1981. The relationship between the motivation of directed and undirected song in the Zebra Finch. Z. Tierpsychol 57, 37-50.

Catchpole, C.K., Leisler, B. & Dittami, J. 1986. Sexual differences in the response of Great Reed Warblers *Acrocephalus arundinaceus* to song structure and repertoire size. Ethology 73, 69-77.

Clayton, N.S. 1987a. Mate choice in male Zebra finches: some effects of cross-fostering. Anim. Behav. 35, 596-597.

Clayton, N.S. 1987b. Song tutor choice in zebra finches. Anim. Behav. 35, 714-721.

Clayton, N.S. 1987c. Song learning in cross-fostered zebra finches: a re-examination of the sensitive phase. Behaviour 102, 67-81.

Clayton, N.S. 1988. Song learning and mate choice in estrildid finches raised by two species. Anim. Behav. 36, 1589-1600.

Clayton, N. S. 1989. The effects of cross-fostering on selective song learning in estrildid finches. Behaviour 109, 163-175.

Clayton, N. S. 1990. Mate choice and pair formation in Timor and Australian Mainland zebra finches. Anim. Behav. 39, 474-480.

Clayton, N. & Bischof, H.-J. 1989. Neurophysiological and behavioral development in birds: song learning as a model system. Naturwisseinschaften 76, 1-5.

Clayton, N. S. & Prove, E. 1989. Song discrimination in female zebra finches and Bengalese finches. Anim. Behav. 38, 352-354.

Cooke, F. & McNally, C. M. 1974. Mate selection and colour preferences in lesser snow geese. Behaviour 111, 151-169.

Cunningham, M. A. & Baker, M. C. 1983. Vocal learning in white-crowned sparrows: Sensitive phase and song dialects. Behav. Ecol. Sociobiol. 13, 259-269.

Eales, L. A. 1985a. Song learning in Zebra Finches. Phd Thesis, University of Sussex.

Eales, L. A. 1985b. Song learning in zebra finches: Some effects of song model availability on what is learnt and when. Anim. Behav. 33, 1293-1300.

Eales, L. A. 1987a. Do zebra finch males that have been raised by another species still tend to select a conspecific song tutor?. Anim. Behav. 35, 1347-1355.

Eales, L. A. 1987b. Song learning in female-raised zebra finches; another look at the sensitive phase. Anim. Behav. 35, 1356-1365.

Eales, L. A. 1989. The influences of visual and vocal interaction on song learning in zebra finches. Anim. Behav. 37, 507-508.

Edwards , T. C. 1989. The ontogeny of diet selection in fledgling ospreys. ecology 70, 881-896.

Evans, S. M. 19 . Aggressive and territorial behaviour in captive zebra finches . Bird Study 17, 28-35.

Farner, D. S. & Serventy, D. L. 1960. The timing of reproduction in the arid regions of Australia. Anat. Rec. 137, 354-370.

Fetherston, I. A. & Burley, N. T. 1990. Do zebra finches prefer to mate with close relatives. Behav. Ecol. Sociobiol. 27, 411-414.

Grant, B. R. 1984. The significance of song variation in a population of Darwin's finches. Behaviour 89, 90-116.

Hötker, H. 1982. Studies of the behaviour of young meadow pipits (*Anthus pratensis*) after fledging. Vogelwelt 103, 1-16.

Immelmann, K. 1962. Beiträge zu einer vergleichenden Biologie australischer Prachtfinken. Zool.Jb.Syst. 90, 1-196.

Immelmann, K. 1965. Australian Finches in Bush and Aviary. Sydney: Angus and Robertson.

Immelmann, K. 1969. Song development in the zebra finch and other estrildid finches. In: Bird Vocalisations. Ed. R.A. Hinde.

Immelmann, K. 1972a. The influence of early experience upon the development of social behaviour in estrildine finches. In: Proc. XV Orn. Congr., Den Haag 1970, pp. 316-338.

Immelmann, K. 1972b. Sexual and other long term aspects of imprinting in birds and other species. In: Advances in the study of behaviour. Vol.4. Academic Press, NY and London.

Immelmann, K. 1975. The evolutionary significance of early experience. In: Function and Evolution in Behaviour Ed. G.Barrends, C.Beer, A.Manning. Clarendon Press, Oxford.

Immelmann, K., Kalberlah, H.H., Rausch, P. & Stahnke, A. 1978. Sexuelle Prägung als möglicher Faktor innerartlicher Isolation beim Zebrafinken. J. Orn. 119, 197-212.

Immelmann, K., Pröve, R., Lassek, R. & Bischof, H-J. 1991. Influence of adult courtship experience on the development of sexual preferences in zebra finch males. Anim. Behav. 42, 83-89.

Immelmann, K. & Suomi, S. J. 1981. Sensitive phases in development. In: Behavioural Development Eds. K.Immelmann, G.W.Barlow, L.Petrinovich, M.Main) C.U.P.

Keast, A. 1958. Intraspecific variation in the Australian finches. Emu 58, 219-246.

Kroodsma, D. E. 1980. Winter wren singing behavior: A pinnacle of song complexity. Condor 82, 357-365.

Kroodsma, D. E. 1984. Songs of the alder flycatcher (*Empidonax alnorum*) and willow flycatcher (*Empidonax traillii*) are innate. Auk 101, 13-24.

Kroodsma, D. E. & Pickert, R. 1980. Environmentally dependent sensitive periods for avian vocal learning. Nature 288, 477-479.

Kroodsma, D. E. & Pickert, R. 1984. Sensitive phases for song learning: Effects of social interaction and individual variation. Anim. Behav. 32, 389-394.

Kruijt, J. P., Bossema, I. & Lammers, G. J. 1982. Effect of early experience and male activity on mate choice in mallard females (*Anas platyrhynchos*). Behaviour 80, 32-43.

Kruijt, J. P. & Meeuwissen, G. B. 1991. Sexual preferences of male zebra finches: effects of early and adult experience. Anim. Behav. 42, 91-102.

Kruijt, J. P., TenCate, C. & Meeuwissen, G. B. 1983. The influence of siblings on the development of sexual preferences of male zebra finches. Developmental Psychobiology 16(3), 233-239.

Lehrman, D. S. 1970. Semantic and conceptual issues in the Nature-Nurture ploblem. In: Development and evolution of behaviour. Essays in memory of TC Schneirla. Ed. Aronsen, Tobach, Lehrman, Rosenblatt. San Francisco. WH Freeman and Co.

Mann, N. I., Slater, P. J. B., Eales, L. A. & Richards, C. 1991. The influence of visual stimuli on song tutor choice in the zebra finch, Taeniopygia guttata. Anim. Behav. 42, 285-293.

Marler, P. 1970. A comparative approach to vocal learning: song development in white-crowned sparrows. J. comp. physiol. Psychol. 71 (Suppl), 1-25.

Marler, P. 1976. Sensory templates in species-specific behavior In: Simpler Networks and Behavior Ed. J.C. Fentress Mass. Sinauer 314-329.

Marler, P. 1987. Sensitive periods and the roles of specific and general sensory stimulation in birdsong learning. In: Imprinting and Cortical Plasticity Eds. J.P. Rauschecker & P. Marler. Wiley, New York.

Marler, P. & Peters, S. 1977. Selective vocal learning in a sparrow. Science 198, 519-521.

Marler, P. & Peters, S. 1982. Developmental overproduction and selective attrition: new processes in the epigenesis of bird song. Dev. Psychobiol. 15, 369-378.

Martin, H. J. 1985. Zebra Finches A complete pet owner's Manual. Barron's Educational Series Inc.

McGregor, P. K. 1980. Song dialects in the corn bunting (*Emberiza calandra*). Z. Tierpsychol. 54, 285-297.

Miller, D. B. 1979a. The acoustic basis for mate recognition by female Zebra Finches (Taeniopygia guttata). Anim. Behav. 27, 376-380.

Miller, D. B. 1979b. Long-term recognition of father's song by female zebra finches. Nature 280, 389-391.

Millington, S. J. & Price, T. D. 1985. Song inheritance and mating patterns in Darwin's finches. Auk 102, 342-346.

Morris, D. 1954. The reproductive behaviour of the zebra finch (*Peophila guttata*) with special reference to pseudofemale behaviour and displacement activities. Behaviour 6, 271-322.

Nicolai, J.1956. Zur Biologie und Ethologie des Gimpels (Pyrrhula pyrrhula L.). Z. Tierpsychol. 13, 93-132.

Nicolai, J. 1959. Familientradition in der Gesangsentwicklung des Gimpels (*Pyrrhula pyrrhula* L.).J. Orn. 100, 39-46.

Nottebohm, F. 1969. The "critical period" for song learning in birds. Ibis 111, 386-387.

Nottebohm, F. 1984. Birdsong as a model in which to study brain processes related to learning. Condor 86, 227-236.

Nottebohm, F. 1989. From bird song to neurogenesis. Sci. Amer. Feb, 56-61.

Nottebohm, F. & Nottebohm, M. E. 1978. Relationship between song repertoire and age in the canary *Serinus canaria*. Z. Tierpsychol. 46, 298-305.
Payne, R. B. 1981. Song learning and social interaction in indigo buntings. Anim. Behav. 29, 688-697.

Payne, R. B. 1985. Behavioral continuity and change in local song populations of village indigobirds *Vidua chalybeata*. Z. Tierpsychol. 70, 1-44.

Petrinovich, L. 1985. Factors influencing song development in the white-crowned sparrow (*Zonotrichia leucophrys*). J. comp. Psychol. 99, 15-29.

Petrinovich, L. & Baptista, L. F. 1987. Song development in the white-crowned sparrow: modification of learned song. Anim. Behav. 35, 961-974.

Schutz, F. 1965. Sexuelle prägung bei Anatiden. Z. Tierpsychol. 22, 50-103.

Slater, P. J. B. 1983. Bird song learning: theme and variations In: Perspectives in Ornithology Ed. GH Bursh & GA Clark. Cambridge University Press, New York

Slater, P. J. B. 1989. Bird song learning: causes and consequences. Ethology Ecology & Evolution 1, 19-46.

Slater, P. J. B. & Clayton, N. S. 1991. Domestication and song learning in zebra finches. Emu 91, 126-128.

Slater, P. J. B., Eales, L. A. & Clayton, N. S. 1988. Song learning in zebra finches: progress and prospects. In: Advances in the Study of Behaviour. 18, 1-34.

Slater, P. J. B. & Ince, S. A. 1982. Song development in chaffinches: what is learnt and when? Ibis 124, 21-26.

Slater, P. J. B., Ince, S. A. & Colgan, P. W. 1980. Chaffinch song types: their frequencies in the population and distribution between the repertoires of different individuals. Behaviour 75, 207-218.

Slater, P. J. B. & Mann, N. I. 1990. Do male zebra finches learn their fathers' songs? TREE 5, 415-417.

Slater, P. J. B. & Richards, C. 1990. Renesting and song learning in the zebra finch, *Taeniopygia guttata*. Anim. Behav. 40, 1191-1192.

Slater, P. J. B., Richards, C. & Mann, N. I. 1991. Song learning in zebra finches exposed to a series of tutors during the sensitive phase. Ethology. 88, 163-171.

Sokal, R. R. & Rohlf, F. J. 1981. Biometry. (Second edition). WH Freeman & Company, San Francisco.

Sonnemann, P. & Sjölander, S. 1977. Effects of cross-fostering on the sexual imprinting of the female zebra finch (*Taeniopygia guttata*). Z. Tierpsychol. 45, 337-348.

Sossinka, R. & Böhner, J. 1980. Song types in the zebra finch (Peophila guttata castanotis). Z. Tierpsychol. 53, 123-132.

Sossinka, R., Prove, E. & Immelmann, K. 1980. Hormonal mechanisms in avian behavior In: 2nd International Symposium on Avian Endocrinology Ed. A Epple & MH Stetson. Academic Press.

Stamps, J., Kus, B., Clark, A. & Arrowood, P. 1990. Social relationships of fledgling budgerigars *Melopsitticus undulatus*. Anim. Behav. 40, 688-700.

Ten Cate, C. 1982. Behavioural differences between Zebra finch and Bengalese Finch (foster) parents raising Zebra Finch offspring. Behaviour 81, 152-172.

Ten Cate, C. 1984. The influence of social relations on the development of species recognition in zebra finch males. Behaviour 91, 263-285.

Ten Cate, C. 1985a. Differences in the interactions between zebra finch and Bengalese finch parents with conspecific versus heterospecific young. Z. Tierpsychol. 67, 58-68.

Ten Cate, C. 1985b. Directed song of male zebra finches as a predictor of intra- and inter- specific social behaviour and pair formation. Behav. Proc. 10, 369-374.

Ten Cate, C. 1986a. Listening behaviour and song learning in zebra finches. Anim. Behav. 34, 1267-1268.

Ten Cate, C. 1986b. Sexual preferences in zebra finch males raised by two species: I. A case of double imprinting. J. Comp. Psychol. 100, 248-252.

Ten Cate, C. 1987. Sexual preferences in zebra finch males raised by two species: II. The internal representation resulting from double imprinting. Anim. Behav. 35, 321-330.

Ten Cate, C. 1988. The causation and development of sex differences in partner preferences. In: ACTA XIX Congressus Internationalis Ornithologici, Vol.1, pp. 938-946. Ed. H.Ouellet, Univ. of Ottawa Press, Ottawa.

Ten Cate, C., Los, L. & Schilperood, L. 1984. The influence of differences in social experience on the development of species recognition in the Zebra Finch. Anim. Behav. 32, 852-860.

Ten Cate, C. & Mug, G. 1984. The development of mate choice in zebra finch females. Behaviour 90, 125-150.

Ten Cate, C. & Slater, P. J. B. 1991. Song learning in zebra finches: how are elements from two tutors integrated?. Anim. Behav. 42, 150-152.

Thielcke-Poltz, H. & Thielcke, G. 1960. Akustisches Lernen verschieden alter schallilierter Amseln (*Turdus merula* L.) und die Entwicklung erlernter Motive ohne und mit kunstlichem Einfluss von Testosteron. Z. Tierpsychol. 17, 211-244.
Thorpe, W. H. 1958. The learning of song patterns by birds, with especial reference to the song of the chaffinch *Fringilla coelebs*. Ibis 100, 535-570.

Walter, M. J. 1973. Effects of parental colouration on the mate preference of the zebra finch *Taeniopygia guttata*. Behaviour 46, 154-173.

Walters, M. J., Collado, D. & Harding, C. F. 1991. Oestrogenic modulation of singing in male zebra finches: differential effects on directed and undirected songs. Anim. Behav. 42, 445-452.

West, M. J. & King, A. P. 1988. Female visual displays affect the development of male song in the cowbird. Nature 334, 244-246.

Williams, H. 1990. Models for song learning in the zebra finch: fathers or others. Anim. Behav. 39, 745-757.

Zann, R. 1984. Structural variation in the Zebra Finch distance call. Z. Tierpsychol. 66, 328-345.

Zann, R. 1985. Slow continuous wing moult of Zebra Finches (*Peophila guttata*) from SE Australia. Ibis 127, 184-196.

Zann, R. 1990. Song and call learning in wild zebra finches in south-east Australia. Anim. Behav. 40, 811-828.